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Sociality: The Behaviour of Group-Living Animals

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‘For Alison, Sammy and Freddy’ (AJWW)
‘To my parents and Kirsty Owen’ (MMW)

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Sociality

1

1.1 Animal Aggregations

Herds, flocks, swarms and shoals provide some of the most visually dramatic phenomena in the natural world. The sight of a mass of individuals turning and twisting in unison is fascinating, almost hypnotic. The spectacle often provokes questions such as ‘how do the animals act as though they were perfectly choreographed?’ or ‘why do they form into these groups?’ Moreover, the tendency of animals to structure their interactions and to integrate into societies is a facet of their behaviour which inspires comparison with ourselves. Researching these and related questions has been a central goal of students of animal behaviour even before such luminaries as Niko Tinbergen and Konrad Lorenz codified and defined the scientific approach to animal behaviour.

If we are to provide answers to such questions, then a necessary first step is to define our terms, particularly since the semantics are occasionally problematic. For example, animals that form groups are commonly referred to as being social. However, this term is controversial in some quarters, since, according to its definition in the Oxford English Dictionary, the adjective ‘social’ refers to a society, an organised community. While many organisms do form highly structured societies, this is not the case for the herds, flocks and shoals mentioned previously, where there is often little evidence of hierarchical structure. The most sophisticated of animal societies are often referred to as eusocial, while in this scheme of categorisation, other species are referred to as presocial, based on their societal characteristics. Unfortunately, the unavoidable implication of this is that many other group-forming animals are not social. For this reason, the word ‘gregarious’ is sometimes preferred for less structured groups.

Other authorities, by contrast, take a much broader view as to what constitutes social behaviour, considering that the term encompasses a diverse range of behaviour but that its defining characteristic is simply that it involves an interaction between animals (Brown 1975). By this definition, sociality is not restricted to the examples of animals that live in groups, although these provide highly visible

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examples of the phenomenon. In their groundbreaking book *Social Foraging Theory*, Giraldeau and Caraco (2000) use the term ‘social’ to refer to the interdependence of foragers as they find and deplete resources and thus influence one another’s costs and benefits. Put another way, individual foragers operate in a dynamic resource landscape whose attributes are constantly in a state of flux as a result of the actions of multiple agents. Nonetheless, the word social has been applied by behavioural ecologists in reference to the tendency of animals to live in groups for some considerable time. Tinbergen (1951) in his seminal work *The Study of Instinct* remarked that ‘An animal is called social when it strives to be in the neighbourhood of fellow members of its species when performing some, or all, of its instinctive activities’. It is in this sense in which we apply the word social throughout this book.

Following on from this, we might ask the apparently simple question ‘what is a social group?’ Providing a definition of a social group that can readily be applied across species has proven difficult, and attempts to do so tend to sacrifice precision in order to promote the inclusion of as many species as possible. For example, E. O. Wilson (1975) defined a group as ‘any set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics’. While such a definition makes intuitive sense, it is essentially qualitative and reflects the difficulty of achieving a universal definition that applies to all species. Animals often form aggregations in nature, sometimes as a result of the temporal and spatial clumping of resources, such as food, water or shelter. For example, a water hole on an African savannah in the dry season is used by animals representing a range of different species, including both herbivores and carnivores. Tinbergen used the analogous example of many moths drawn to a lamp. Neither case could be described as a social aggregation. The fundamental quality that distinguishes a social group is that it forms and is maintained by social attraction between group members. Hence, a working definition of a social group is one where two or more individuals maintain proximity in space and time through the mechanism of social attraction. Although animals with similar requirements and motivations moving through a heterogeneous resource landscape may display some synchrony in their patterns of activity, leading to the formation of aggregations, studies have demonstrated the importance of social attraction over and above activity synchrony to the maintenance of cohesive groups (Michelena et al. 2008). From a functional perspective, this social attraction and the resultant formation of a social group of mutually attracted individuals confer to all group members some evolutionary advantage, such as access to information, the reduction in the risk of predation or access to foraging benefits (see Chap. 4).

1.2 Different Types of Social Group

Despite the fact that we are able to identify social attraction as the fundamental unifying mechanism underlying social groups, there is an apparently bewildering diversity in the expression of sociality both within and between animal species. To

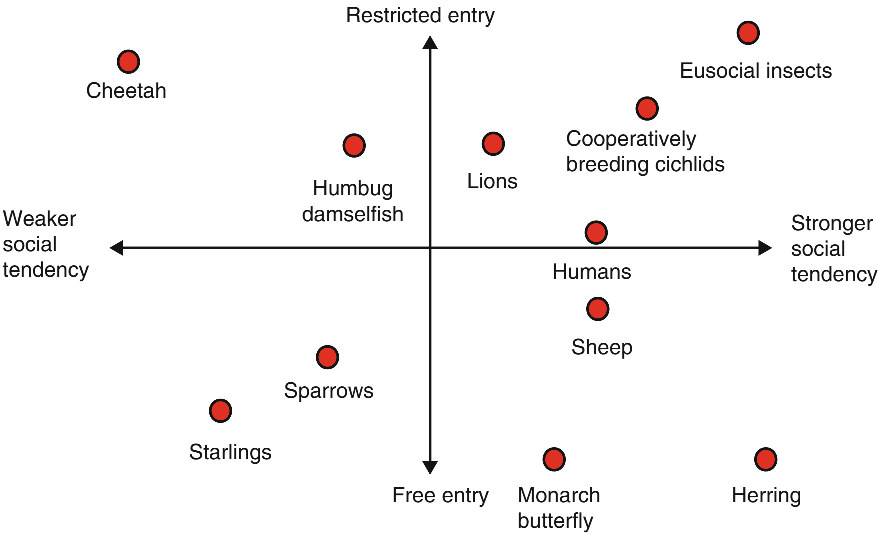

Fig. 1.1 Schematic representation of patterns of sociality among different animal species according to their social tendency and the level of entry restrictions to their group. This initial diagram is qualitative, and the relative positions of species are based on no more than the authors' opinions. Nonetheless, the positions could be quantified: social tendency may be measured by examining the proportion of active time individuals of a given species spend within a given distance of one or more conspecifics; the entry characteristics of a group may be measured in a number of different ways, including consistency of group membership over time or the aggression directed towards transient conspecifics

try to make sense of this diversity, we might consider the ways in which animal groups differ from one another. Fundamentally, we consider that these differences arise through variation in two main parameters: firstly, the tendency of members of a given species to associate with conspecifics and, secondly, the organisation of the social group itself (Fig. 1.1).

1.3 Social Group Characteristics I: Social Tendency

In the first instance, the tendency to associate with conspecifics varies considerably among species, where some species are only weakly social, or social at some times, but not at others, while others are highly and intrinsically social. These are sometimes categorised, respectively, as facultatively and obligatorily social species; however, this terminology can create the unhelpful impression of a clear dichotomy between facultatively and obligatorily social species. As Partridge (1982) noted, the groups formed by species with different social tendencies are typically organised according to the same principles, making strict categories essentially meaningless. Instead, the difference among species relates to the tendency of individuals to associate with conspecifics, which varies along a continuum among species and even within species. While there are some species, such as eusocial insects, which spend almost their entire lives in close proximity to and interacting with conspecifics, there are many other social species where individuals interact with conspecifics under some circumstances, or at particular stages in their life history, but not at others.

To an extent, variation along this scale covaries with relatedness – many highly social animals live in kin groups, and the fitness of individuals of such species is entirely dependent on group living. A single eusocial bee is able to scout and to forage episodically, but it is reliant upon the social group for its survival. Eusocial organisms are not the only organisms to display so-called obligate sociality; such a fundamental reliance upon the social group is also a feature of animals that are sometimes described as 'presocial' – those that display some, but not all, of the characteristic traits of eusocial organisms. For example, wolves (*Canis lupus*) are often considered to be a presocial species (or even by some to be eusocial). While the proverbial 'lone wolf' does occur, wolves are typically highly social and form packs, usually based on an adult pair and their offspring of various ages. It is important to note, though, that there are also obligatorily social species which do not fulfil the criteria to be described as presocial, and which do not form into exclusive kin groups, such as herring (*Clupea* spp.), and krill, which form among the largest animal aggregations of all, numbering up to a trillion separate organisms and which may be viewed from space.

Other social animals may engage in fewer social interactions, and to be less reliant upon those interactions than obligatorily social species, however, group living remains fundamental to their lifetime fitness. Although a few species live in enormous groups: colonies of driver ants may reach up to 22 million in number, while groups of the now extinct Rocky Mountain locust (*Melanoplus spretus*) were estimated to reach 3.5 trillion (Dornhaus et al. 2012), most animal groups are fairly small. A number of authors have noted the paradox that, when examining the group size distributions of social species, singletons or very small groups are typically the most frequently observed. Overall, the frequency distribution of group size in many social species tends to follow a power law relationship (Bonabeau et al. 1999; Okubo 1986). Hence, animals that are often thought to be social in fact spend significant periods of their lives alone. A sheep, or a stickleback, for instance, is obviously fully equipped to spend its existence without the presence of conspecifics (with the exception of the need to reproduce!), yet both species, and many like them, obtain a considerable benefit from aggregating with conspecifics for at least part of their lives.

Of course, variation among different species in their tendency to associate with conspecifics is only part of the overall picture. Individual members of a social species can vary considerably in their sociability, despite a lack of immediately obvious proximate or ultimate explanations. This phenomenon has provided one of the most fruitful areas for research in the field of animal social behaviour in recent years, both in terms of gathering new insights into the genetic, neural and physiological bases of social behaviour and into consistent individual differences in the expression of behaviour, often referred to as animal personality. In addition to this, individual animals show differences in their social tendencies according to myriad other factors. For example, the social and reproductive strategies of the sexes in many mammals are not closely aligned, which often leads to the formation of social groups of females and the isolation of males. Similarly, individuals vary in the extent to which they are social according to their age or life history stage. Many fish and amphibian species, for example, are social early in life, but gradually become more solitary as they age. Social caterpillars form perhaps the most dramatic examples of this, being highly social prior to metamorphosis and solitary thereafter. Animals may be social at certain times of day, but not at others, for example, fish shoals break up at dusk and reform at dawn. Individuals may adopt sociality to a greater or lesser extent according to their immediate environment and in particular the level of threat. Finally, many studies have examined differences in sociality among populations. We return to the fascinating questions of how and why sociality varies among individuals in later chapters.

1.4 Social Group Characteristics II: Social Structures and Organisation

Differences in the structure and organisation of social groups among species form our second parameter. For example, social groups vary according to the stability of group membership over time, which reflects whether they are open or closed to new conspecific members. Again this has to be viewed as a continuum, rather than as a set of discrete categories; however, we can place so-called restricted entry groups at one end of this scale and free entry groups at the other. Restricted entry groups tend to be characterised by extremely stable group membership, and members often aggressively repel outsiders who attempt to join. In many cases, such groups are composed of related individuals as is the case with the matrilineal groups that are characteristic of many mammals. Eusocial insects provide us with some of the most remarkable examples of animal societies. The term eusocial indicates specific defined characteristics including the overlap of different generations within the group, the division of reproduction to a small proportion of the group and cooperative care of young (Wilson 1971). Wilson and other authors have defined a number of other categorisations based on these traits. For example, presocial is used to describe animal societies which exhibit a combination of two or less of the three traits and which are often seen as evolutionary steps on the way to eusociality (see Wilson 1971 for definitions).

Not all restricted entry groups are composed of kin, however. Social groups of damselfish have very stable membership over time and energetically exclude outsiders (Buston et al. 2009; Jordan et al. 2010). These groups typically have low within-group coefficients of relatedness. In other species, particularly some primates, the basic social unit is a reproductive family group, and entry to this group, while not closed, is certainly restricted. Similarly, some social groups may effectively restrict entry by penalising new members. For example, in some cases, especially in groups with a stable hierarchy, it is possible for a newcomer to join a group of conspecifics, but the cost to that individual is that it has to accept low social status, at least initially. This has been documented in flocks of siskins (*Carduelis spinus*) where new group members are forced to adopt a subordinate role in the group hierarchy (Senar et al. 1990).

Other species place no restriction on membership and group composition is often much more fluid. This is the case with flocks of some species of birds and fish shoals, among others. For example, a flock of birds may vary in terms of its absolute size and in terms of its membership as different individuals join and leave. Yet despite the apparently loose social organisation of such species, there is evidence to suggest that the larger group may comprise a mosaic of smaller subgroups comprising particular individuals, who associate over longer periods, so that patterns of association between members of the local population are non-random (Pavlov and Kasumyan 2000).

1.4.1 The Dynamics of Social Organisation in Animal Populations

A major feature of vertebrate social organisation in particular is the ongoing process by which individuals, or smaller groups, coalesce into larger groups, which in turn split into smaller groups. The process repeats over time in what is known as a fission-fusion system to reflect the fluctuating nature of group size and composition (Aureli et al. 2008; Kummer 1971). Fission-fusion dynamics have been studied and reported primarily in vertebrate species, particularly mammals, including cetaceans (Lusseau 2003), carnivores (Schaller 1972; Wolf et al. 2007), bats (Popa-Lisseanu et al. 2008), ungulates (Aycrigg and Porter 1997; Cross et al. 2005), elephants (Wittemyer et al. 2005) and primates (Symington 1990), but also in birds (Silk et al. 2014) and fish (Croft et al. 2005; Hoare et al. 2004).

Fission and fusion provide a highly responsive means for social animals to adapt to changes in proximate social and environmental conditions (Chapman 1990; Sueur et al. 2011a). For example, under circumstances where the threat of predation is high, large groups may be favoured, while smaller groups may be favoured during foraging, especially in a patchy environment. Determining the relative roles played by environmental factors, such as resource distribution, and by socially mediated decisions of individuals to remain with or to leave a group is a current challenge in social behaviour research. Furthermore, groups may merge or split through self-organised processes, such as activity synchrony (Conradt and Roper 2000) and basic locomotive speed (Krause et al. 2005), and/or according to ecological heterogeneity and differences among individuals (Couzin 2006; Ramos-Fernandez et al. 2006). Understanding how fission-fusion dynamics shape patterns of association at the individual level and shape demographic processes at the population level is currently being tackled using social network analysis. Research into this area of the social behaviour of animals has major implications for our understanding of patterns of gene flow (Altmann et al. 1996), disease transmission (Croft et al. 2011; Griffin and Nunn 2012) and the spread of information and innovation throughout populations (McComb et al. 2001; Vital and Martins 2009).

While fission-fusion dynamics describe an iterative process of coalition and separation in the social organisation of many species, there are key differences between species. In particular, there are differences in the extent to which groups assort and reassort. Among some species exhibiting fission-fusion social dynamics, such as many birds or fish, each individual is able to leave, or to join, any group (Wilson et al. 2014). In other species, the movement of individuals between groups is constrained. For example, in some primate societies, a larger group is composed of many smaller subgroups, which in turn comprise just a few individuals. These subgroups often remain together for long periods of time, and subgroups seldom exchange individual members.

1.4.2 Multilevel Societies

The term multilevel society refers to two or more nested, hierarchical tiers within the social organisation of a species. Each individual is a member of a basic social unit, and that unit in turn is part of another, larger, higher tier, which in turn may form part of yet another tier. For example, studies on some primate societies have identified an overall troop of animals that is subdivided into smaller social units, which in primate society typically comprises a single, adult male and one or more females. These units sometimes coalesce into larger groups, or bands, which form an intermediate layer between the basic social unit and the overall troop (Dunbar and Dunbar 1975; Grueter et al. 2012; Grueter and Zinner 2004; Zhang et al. 2012). While the subgroup is the basic unit of a multilevel society, such units may coalesce into larger groups under the influence of increased threat, either from predators or even from conspecifics, particularly through male infanticide, to facilitate territory defence, promote allocare or enable mating opportunities (Grueter and van Schaik 2010; Rubenstein and Hack 2004).

Multilevel societies are considered by some researchers as a specific form of fission-fusion society, but by other authorities to be entirely distinct. While multilevel societies do exhibit fission-fusion social dynamics, when fission does occur, larger groups tend to split into their constituent subunits, rather than randomly. As a result, we can draw a distinction between a true multilevel society and a society which simply exhibits fission-fusion dynamics: in a multilevel society, the composition of each subunit is highly stable over time in terms of its size and membership, while in a fission-fusion society, group composition is much less predictable, either in terms of size or membership (Chapman et al. 1993; Symington 1990).

Multilevel societies are primarily a phenomenon of mammal social organisation and are particularly widespread among primates. However, they are also found in cetaceans (Whitehead et al. 1991), plains zebras (Rubenstein and Hack 2004) and elephants (Wittemyer et al. 2005). Zebras (*Equus burchelli*) provide one of the simplest forms of multilevel society, since it only has two levels: the core breeding unit, usually of a single male and several females, and the larger herd. In elephants (*Loxodonta africana*), Wittemyer and co-workers (2005; Wittemyer et al. 2009) define a series of social tiers: the basic unit is a mature female and her offspring, which often associate into family groups at the next level. These family groups comprise higher level groups on the basis of relatedness and social bonding. The social organisation of sperm whales (*Physeter macrocephalus*) differs across populations; however, the basic social unit comprises up to ten females and juveniles (Whitehead et al. 2012). These units may associate with others in groups, but this is a highly selective process, and the patterns of association of units in groups are not random (Whitehead 2003). The groups are part of the higher social tier, sometimes referred to as the clan, which may be made up of thousands of individual whales, united by clan-specific patterns of vocalisations (Rendell and Whitehead 2003).

1.5 The Scope of This Book

The aim of this book is to provide a synthesis of the many diverse strands involved in the current work on animal social behaviour. In Chap. 2, we consider social recognition and its founding role in the social organisation of species with specific reference to the process of recognition and the sensory basis of the phenomenon.

Collective behaviour has been the subject of considerable, multidisciplinary, interest for over a decade now. In Chap. 3, we examine how individual animals interact and how these localised interactions give rise to emergent patterns at the level of their groups. We return to the topic in Chap. 8 to describe the collective functioning of groups in terms of collective decision-making and swarm intelligence.

Much consideration has been given to the payoffs for animals in social groups and we examine the current state of our knowledge on the costs and benefits of sociality in Chaps. 4 and 5. This leads into the examination of the way that these benefits and costs may vary among group members in Chap. 6, particularly in relation to dominance relationships and the relative positions occupied by individuals within groups. Then, in Chap. 7, we consider how group size affects individual payoffs and group function and how phenomena such as social facilitation and social conformity act to shape these costs and benefits.

In Chap. 9, we examine how sociality develops and changes throughout the lifetime of an individual according to intrinsic and extrinsic ontogenetic factors. In Chap. 10, we consider the evolution of sociality, from interindividual difference in social tendency through to social cognition and culture. Finally, we present our conclusions on the current state of research into the topic, including our suggestions for future developments in this field.

Mechanisms: Social Recognition and Social Organisation

2

2.1 Introduction

Social organisation in animals takes many forms. It includes assemblages of territorial animals, dominance hierarchies and social groups, among other things. The basic tenet that underlies these forms of social organisation is that animals adapt their responses to the different individuals that they encounter according to some recognised characteristic. For example, an individual may be socially attracted to some, but may ignore others; it may defer to some, or it may dominate others. Consequently, all forms of social organisation are reliant upon social recognition, which is the ability of an individual to discriminate among other animals that it encounters within its environment and to bias its behaviour accordingly, directing the appropriate behaviour towards the appropriate individual. Even mass displays of self-organised, collective phenomena typically occur in flocks, swarms or shoals of a single species, or at least dominated by a single species, implying, at the very least, basic recognition and discrimination of conspecifics from heterospecifics. In terms of group-living animals, the level of structure within the social organisation of a species is reliant upon a suite of interacting and often dynamic factors (see Chap. 1). Thus, their social organisation may be highly structured in time and space or comparatively evanescent. Animals in many instances form groups with kin or with familiar individuals. In doing so, they potentially gain access to inclusive fitness benefits or to the enhanced antipredator, foraging or social learning benefits that have been described for individuals in such groups. Moreover, social organisation can feed back to strengthen social recognition – animals that spend greater time in association may learn each other's identity with increasing specificity – hence, there is an interrelationship of social recognition and social organisation, both within the lifetime of an animal and most especially throughout evolutionary time. The challenges posed by living among conspecifics in social groups have given rise to the development of cognitive abilities relating to communication, social learning and the development of culture.

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2.2 What Is Social Recognition?

Recognition is the process of identifying other animals, to a greater or lesser resolution, based on the detection of cues that arise from them. It governs social interactions among animals, underpinning social organisation and ultimately shaping the process of evolution (Sherman et al. 1997). The study of social recognition is therefore fundamental to our understanding of animal social behaviour. While the underlying neurological and biochemical facets of recognition may be complex, the basic sequence of the process of recognition is relatively straightforward to characterise. Sherman et al. (1997) described this process by referring to three sequential components: the production component, the perception component and the action component. The production component refers to the production of cues by an animal that can be used by another individual for recognition. Various terms are used to refer to the cue-producing individual – for example, Sherman et al. referred to this individual as the 'actor', while others have used 'signaller' or 'sender'. For the sake of consistency, we will use 'sender' (sensu Gherardi et al. 2012). The crucial point to make at this stage is that while the production of cues by the sender may be deliberate and intentional, very often they are not; hence, recognition is not a form of signalling, which implies an active and deliberate communication process. Atema (1996) memorably described living organisms as 'leaky bags' since they constantly (though involuntarily) express chemical cues as a by-product of metabolic processes. The second stage of Sherman's sequence, the perception component, describes the detection of the sender's cues by another individual. Again, many terms have been used for the individual detecting the cues; however, we once again follow the lead of Gherardi et al. (2012) and refer to these individuals at 'receivers'. During the perception component, the receiver detects cues arising from the sender and assesses the sender by comparing the cues that it detects to a 'recognition template' (Mateo 2004). Depending on the type and quality of the cues that it detects, and the sophistication of its recognition template, the receiver may be able to achieve some level of discrimination to the point that it is able to recognise characteristics of the sender or even the specific individual identity of the sender. The third stage of Sherman's sequence is the action component, wherein the receiver adjusts its behaviour according to the information that has been acquired from the sender (Liebert and Starks 2004).

2.3 Different Levels of Specificity of Social Recognition

The patterns of social organisation observed in animal populations in nature are the outcome of social recognition between members of that population. The extent to which animals are able to recognise and discriminate between conspecifics varies considerably among species. While some species are capable only of the most basic levels of recognition, others are able to achieve a high degree of specificity. The variation between species can be explained both by the cognitive ability of the species in question and the costs and benefits associated with the ability to recognise conspecifics

(Reeve 1989; Tibbetts and Dale 2007). This specificity of social recognition ranges from the relatively simple categorisations of conspecific/heterospecific to the more complex discernment of subsets of the local population, including the ability to determine kin from non-kin, all the way to the ability to identify particular individuals. Tibbetts and Dale (2007) make the distinction between two primary levels of recognition: class-level recognition and ‘true’ individual recognition. Class-level recognition is a broad category which refers to the ability of receivers to assort senders into categories, such as ‘kin’ or ‘non-kin’, ‘conspecific’ or ‘heterospecific’. Essentially, it encompasses all levels of social recognition below that of individual recognition. Archawaronon et al. (1991) took a more nuanced approach to this by making the distinction between a basic, binary form of categorisation and the more sophisticated ability of animals to assort conspecifics into more specific categories, such as (in the case of kin recognition) ‘sib’, ‘half-sib’, ‘parent’, ‘offspring’, etc. Nonetheless, the main difference between these two approaches may be semantic, since both acknowledge the ability of animals to discriminate between subsets of their social environment.

Recognition may also involve processing of different facets of sender information such that the sender may be allocated to progressively more specific categories. As an example of this, imagine that I encounter another person in the street. At a distance, I might first determine that the approaching organism is a human, and then as it approaches, I can determine that it is male, that I am unfamiliar with him personally, but, as I hear him speak, that I recognise his accent and can approximate where he is from. Similarly, receivers may sometimes simultaneously perform more than one class of recognition and recognise a sender as, for example, a familiar kin individual (Frommen et al. 2007; Cheney and Seyfarth 1999; Bergman et al. 2003).

The most specific form of recognition involves the identification of individuals. The ability to discriminate between and behave differently to multiple different individuals is sometimes referred to in the literature as ‘true’ individual recognition, to distinguish it from cases where animals discriminate between two conspecifics in a dyadic situation, for example, when presented with two potential rivals. The ability to discriminate between these two rivals does mean that animals are differentiating between two individuals, but does not imply individual recognition (Wiley 2013). Specifically, true individual recognition is said to occur where an animal learns the unique identifying characteristics of another individual and allocates those characteristics to the specific identity of that individual and the information it holds on that individual based on their previous interactions, for example, its social status or its home range. By contrast, class-level recognition, where a receiver identifies the characteristics of the sender, but fails to allocate a unique identity to it, instead simply allocates it to a class or category (Sherman et al. 1997; Tibbetts and Dale 2007). Interesting questions remain to be examined in the study of individual recognition, including the extent to which individual recognition is dependent upon location and context (Wiley 2013). Evidence suggests that, in some species, individual recognition is most likely to occur when the receiver encounters the sender in the ‘correct’ location or the ‘correct’ context and can weaken or fail if the encounter occurs outside of the expected context or location, even in human recognition (Shapiro and Penrod 1986).

Generally, the resolution to which animals are capable of identifying others relates to their ecology and to the structure of their societies. The evolution of increased social complexity goes hand in hand with the development of increasingly sophisticated social recognition abilities. For non-hierarchical animals that live in enormous fission-fusion groups, there is likely little value to learning individual identities of conspecifics, whereas for animals that live in stable societies and where individuals repeatedly encounter each other across each day and over their lifetimes, there is a clear benefit to learning and recalling the identities of group mates. Indeed, this can be crucial for the maintenance of bonds and affiliations in such societies and the development of phenomena such as reciprocal altruism.

2.3.1 Basic Recognition

For many animal interactions, however, only a relatively basic level of discrimination is required. The categorisation of self *versus* non-self is of course a consideration for the immune system of many animals, but also in some specialised social interactions, such as that which occurs between clownfish (*Amphiprion* spp.) and their host anemones. The question of how clownfish and also some species of crustaceans are able to take refuge within the tentacles of an anemone without being stung is one that has long fascinated biologists (Davenport and Norris 1958; Lubbock 1980). While we still do not know the exact mechanism, it is generally thought that the mucus of the clownfish acts to prevent non-self recognition by the anemone and hence prevents the discharge of stinging nematocysts (Mebs 2009).

For species which live in large and highly dynamic social systems, such as starlings, some ungulates, especially during migrations, and fish such as sardines and herring, social recognition may be relevant merely to distinguish conspecifics from heterospecifics. By identifying conspecifics, animals can exercise an active preference to assort with others of their own kind, which carries with it many potential benefits, including obtaining relevant information. For example, given a choice to assort with conspecifics or with heterospecifics in experimental set-ups, shoaling fish species typically manifest a strong preference for conspecifics (Keenleyside 1955). However, besides this active preference for conspecifics, animals may passively assort into single-species groups through a process of self-organisation based on similar locomotion speeds and activity synchrony. This passive assortment does not need to involve any form of social recognition. Nonetheless, the ‘active preference’ and the ‘passive assortment’ explanations are not mutually exclusive – indeed they are likely to operate in tandem in the formation of animal groups.

Social recognition to the level of species is vital to the ecology of species which disperse during early life, since it allows them to home in on the cues of conspecifics and to use these as a proxy for suitable habitat patches in which to settle. In marine systems, many invertebrates and nearly all coral reef fishes feature in their life history a larval stage which lives and feeds in the plankton. As the young animal develops, it must locate some suitable habitat to undergo the next phase of its life, as an adult. Navigation under these circumstances is achieved partly by detecting and moving towards the chemical cues of adult conspecifics. Prendergast and colleagues (2008) studied the behaviour of cyprid larvae of the barnacle, *Semibalanus balanoides*, and concluded that their settlement behaviour was strongly affected by the presence of adult conspecific cues in the local environment. Lecchini and Nakamura (2013) obtained similar results in a broad-ranging study encompassing larval cephalopods, crustaceans and fish.

2.3.2 Recognition of Kin and Familiars

For most social species, however, a greater degree of discrimination is necessary than the simple categorisation of others into conspecifics and heterospecifics. In particular, kin recognition is a fundamental requirement if animals are to bias their behaviour in favour of kin (sometimes referred to as nepotism) and to avoid inbreeding (Hamilton 1964; Sherman and Holmes 1985; Fletcher and Michener 1987; Hepper 1991). For eusocial insects, it is necessary to discriminate between colony members and non-colony members in order to prevent the latter invading the colony, exploiting valuable resources and eroding the high levels of relatedness that underpin the functioning of such societies. Yet while social insects are capable of making accurate assessments of whether an individual does or does not belong to their own colony, there is surprisingly little evidence to support their ability to discriminate among individuals according to relatedness within their own colonies (Strassmann et al. 1997; Holldobler and Wilson 2008; see also Leadbeater et al. 2014). Nonetheless, other arthropods do show a clear ability to recognise kin, including juvenile spiders, *Stegodyphus lineatus*, which are socially attracted to the cues of siblings, and cockroaches, *Blattella germanica*, which preferentially associate with kin (Johannesen and Lubin 2001; Lihoreau and Rivault 2009; Ruch et al. 2009; Grinsted et al. 2011). The functional benefit of associating with kin was examined by Ruch and colleagues (2014) in a study on the hunting behaviour of crab spiders (*Diaea ergandros*; see Fig. 2.1). The authors found that groups comprised entirely of kin were more successful at hunting than those which incorporated unrelated outsiders and that this translated into greater gains in mass in the kin groups.

The ability to discriminate kin from non-kin does not necessarily influence social behaviour or association preferences. There is little evidence among shoaling fish species for the existence of kin groups (although see Pouyaud et al. 1999), although the ability to discriminate kin is widespread. Amphibians are also able to identify kin; however, this can in some cases mediate their association preferences and lead to the formation of kin groups of larvae (Waldman and Adler 1979; Blaustein and Waldman 1992). Association with kin is an intrinsic part of the social systems of many mammals, including lions, wolves and many cetaceans. Matrilineal groups are a common phenomenon among mammals. Female relatives form the main social unit, while juvenile male offspring disperse upon maturity, while female offspring remain with the group, which can comprise three or even more generations in long-lived animals, such as elephants and orcas. Cooperative behaviours and the potential for social

Fig. 2.1 Individually marked crab spiders (*Diaea ergandros*) overwhelm a fly. The spiders are more successful at hunting when they hunt in groups of kin (From Ruch et al. 2014)

learning and cultural transmission are all features of such long-lasting kin groups, all of which provide vital fitness benefits for group members. In the case of orcas (*Orcinus orca*), females exhibit an extended menopause, sometimes living for decades beyond the end of their reproductive lives. The evolutionary explanation for this rests with the greater survivorship shown by younger members of groups featuring older female kin (Foster et al. 2012). Adult male mammals are often solitary after reaching maturity, or following their dispersal from natal groups, but there is evidence that brothers may associate in pairs or small bands in order to hunt more effectively, as is the case in cheetahs (*Acinonyx jubatus*), or to cooperate in usurping other males and to take control control of an existing social group, as occurs in lions (*Panthera leo*).

Belding's ground squirrels (*Urocitellus beldingi*) are group-living rodents that occur in alpine regions in the United States and that have provided an extremely fruitful system for the study of kin recognition and nepotism (Holmes and Sherman 1982; Holmes 1994; Mateo 2006). Female squirrels tend to live in close proximity to other female relatives and their offspring. Since broods tend to be multiply sired, there is a diverse pattern of relatedness among individuals, and this intricacy of squirrel society may help to explain their kin recognition abilities and the nepotistic patterns of alarm calling and infanticide and the expression of association preferences for siblings found in this species (Holmes 1994).

Kin groups can also be found among mammal and bird species that exhibit cooperative breeding, such as meerkats and Florida scrub jays (*Aphelocoma coerulescens*). Such groups comprise both reproductive and nonreproductive adults, which assist the other group members in raising offspring. Typically, such groups are composed of close relatives; hence, these helpers, despite not producing their own offspring, are able to increase their own inclusive fitness indirectly by raising nieces, nephews, cousins, etc.. Evidence in birds, however, suggests that in the many examples of cooperative breeding that have been documented in this taxon, the ability of helpers to discriminate siblings and their half-siblings, or even kin from non-kin, when deciding which chicks to provision is based on context-dependent associative learning (Komdeur and Hatchwell 1999). In other words, the rule of thumb used by helpers may simply be that if a chick is in the nest, then it is likely to be kin and they should provision it. While this lack of precision may pose questions as to the evolutionary basis of such behaviour, there are benefits to helpers beyond inclusive fitness, in particular the possibility of acquiring status, parenting experience or the territory at some later stage (Lancaster 1971; Zahavi 1977; Woolfenden and Fitzpatrick 1978).

While the formation of kin groups is most often the outcome of philopatry and the tendency of some animals to remain with their parents into adulthood, the application of social network approaches allows greater insight to individual patterns of association, as opposed to the group-level metrics that have often been used in the past. Using social networks to study a foraging group of barnacle geese (*Branta leucopsis*), Kurvers and co-workers (2013) revealed association patterns among close kin. Sueur et al. (2011a) examined social network structures in macaques, focussing on two socially tolerant species, crested black macaques and Tonkean macaques (*Macaca nigra* and *Macaca tonkeana*), and two less socially tolerant species, rhesus macaques and Japanese macaques (*Macaca mulatta* and *Macaca fuscata*). While kin associations are, to an extent, a feature of all these species' social organisation, the network ties among kin in *M. mulatta* and *M. fuscata* were stronger than in the socially tolerant species, which suggests the possibility of greater nepotism in these species.

Aside from relatedness, the other key element that shapes the interactions of animals within a population is familiarity, which refers generally to the recognition of unrelated individuals. However, there is no consensus on the mechanism underpinning familiarity that applies generally across taxa. Generally, authors imply individual recognition on the basis of prior social experience. However, most examples of familiarity arguably involve the binary categorisation of conspecifics into classes – familiar and unfamiliar – rather than the more cognitively complex 'true' individual recognition, although it can be difficult in practice to separate the two: some examples of familiarity in the literature may be based on true individual recognition and others based on the recognition of a more general, group-specific label. According to the definition of individual recognition proposed by Tibbetts and Dale (2007), to be considered 'true' individual recognition, the sender's cue, the receiver's template and its response to the sender should each be unique and specific to that individual sender. These aspects are seldom tested explicitly as part of such studies on familiarity, which are typically concerned with the functional aspects of familiarity, rather than its mechanistic basis. An exception to this is the study by Ward et al. (2009), which examined whether two species of fish, sticklebacks (*Gasterosteus aculeatus*) and guppies (*Poecilia reticulata*), which are both known to associate preferentially with familiar conspecifics, investigated recognition of familiars via a non-specific group-level label and a more specific form of recognition based on prior social interactions. While sticklebacks were able to use only the general, group-level label for recognition, guppies were able to use both that and the more specific means of recognition. The difference between these species recognition capabilities was ascribed to differences in ecology between the species, since sticklebacks from the populations in question have a less structured social environment encompassing more animals, so rely on general recognition mechanisms.

In a social context, familiarity has been studied extensively in the context of the ‘dear enemy’ effect, wherein familiar holders of adjoining territories appear to declare a truce to focus their attentions on unfamiliar interlopers (Jaeger 1981). Beyond this, familiarity does appear to play a significant role in structuring the social interactions between conspecifics across taxa, with individuals associating with or showing preferential behaviour for familiar individuals in mammals (Boissy and Dumont 2002), birds (Senar et al. 1990), reptiles (Bull et al. 2000), fish (Griffiths 2003; Ward and Hart 2003), insects (Peso and Richards 2010), arachnids (Muleta and Schausberger 2013) and crustaceans (Webster et al. 2008). The diverse range of species that manifest such preferences hints at the existence of considerable benefits, and indeed many such benefits have been reported, including reductions in competition between familiars (Utne-Palm and Hart 2000) and reduction in aggression (Hojesjo et al. 1998; Seppa et al. 2001), which allows animals to concentrate their attentions on more profitable activities (e.g. Griffiths et al. 2004; Strodl and Schausberger 2013), to increase their foraging efficiency (Ward and Hart 2005; Strodl and Schausberger 2012) and to increase the efficiency of social information transfer and social learning (Swaney et al. 2001).

2.3.3 Individual Recognition

Individual recognition involves the perception by a receiver of unique and distinct cues from a sender, the association of these with the specific identity of that individual sender and the expression of a distinct pattern of behaviour towards the sender (Beecher 1989; Gheusi et al. 1994; Tibbetts and Dale 2007; see also Steiger and Mueller 2008). True individual recognition is therefore a relatively complex cognitive process (Mateo 2004; Beecher 1989). For animals that live in relatively stable groups, the ability to recognise and discriminate among individuals allows intricate structuring of social interactions based on the recall of previous interactions; it can allow for the possibility of reciprocity, promoting the formation of long-term alliances and ultimately stabilising the social environment. Individual recognition, like more general kin recognition, can lead to the biasing of behaviour in favour of particular conspecifics. Foraging brown-throated conures (*Aratinga pertinax*) appear to call to recruit familiar, overflying individuals to food patches, suggesting the potential for the development of cooperative behaviour in this species (Buhrman-Deever et al. 2008).

The extent to which animals are able to perform long-term social recognition, and to recognise many different individuals, is likely a function both of the cognitive ability of the animal and the dynamics of the social system. For species that live in fission-fusion societies where interactions between specific individuals may be periodically repeated, but not necessarily frequently, some form of long-term social memory may be advantageous. A study on the ability of bottlenose dolphins (*Tursiops truncatus*) in captivity to recall former associates indicated that these animals are capable of retaining individual recognition for at least 20 years (Bruck 2013). For relatively short-lived animals, or those with a lower probability of re-encountering individuals over an extended period, the benefits of forming long-term social memories are arguably reduced (although see Insley 2000). Belding's ground squirrels undergo up to 8 months of hibernation and, over the course of this time, lose their ability to recognise non-kin individuals that they were reared with (Mateo 2010). Long-term recognition may also be more of a feature of animals that live in stable social groups, rather than those which live in more fluid social environments. Clownfish (*Amphiprion bicinctus*), which live in fixed social groups, retain the ability to recognise their mates after a separation of 30 days (Fricke 1973), while the ability of sticklebacks to recall familiars decays over the course of 1–2 weeks (Utne-Palm and Hart 2000). There have been comparatively few studies of individual recognition in invertebrates; however, Gherardi and colleagues (2005) showed that the long-clawed hermit crab (*Pagurus longicarpus*) is capable of individual recognition of conspecifics and that the information is retained for up to 4 days based on a 30 min exposure.

Similarly, animals that repeatedly encounter a small number of conspecifics may benefit by being able to recall those individuals. African elephants have been estimated to be able to recognise at least 100 different individual conspecifics based on their responses to playback experiments (McComb et al. 2000), while sheep are able to recognise at minimum 50 different individuals based solely on the presentation of photographic images (Kendrick et al. 2001). In a study on the association preferences for familiar individuals in fish, Griffiths and Magurran (1997b) reported an upper limit of around 40 on the number of individuals that female guppies were capable of learning.

2.4 Cues and Templates Used in Social Recognition

The concept of a recognition template, a representation of certain key characteristics that might be used to identify others, is at the heart of much research into recognition systems. This recognition template may be genetically determined, providing the receiver with an innate ability to recognise a given cue, such as is the case with pheromonal communication. Alternatively, the recognition template may be more flexible, reflecting the dynamic nature of many cues that are involved in recognition. In such cases, the template may be generated by learning or through self-referencing where a receiver matches its own cues to that of a sender. Recognition systems, as in other contexts within the field of animal communication, may be subject to conflict. For example, the sender may attempt to manipulate the receiver in order to exploit it. There are many examples of this among social insects where non-colony members have evolved means of interfering with the recognition systems of a host species in order to gain access to a colony. Generally, however, the achievement of unambiguous social recognition among conspecifics is beneficial to both sender and receiver. This favours the development of clear labels to facilitate recognition (Mateo 2004).

The cues used in social recognition may be grouped into four main categories: context-based associative learning, genotype matching, phenotype matching and learned individual characteristics (Bradbury and Vehrencamp 1998). These are not mutually exclusive, and indeed animals may benefit by using more than one category in order to facilitate accurate social recognition. Context-based social recognition is most often founded upon an associative learning process, linking an animal with a spatial feature (such as a burrow or a nest site). A particular example of this is the rule of thumb adopted by parental animals which use cues based on location to 'recognise' their offspring; in other words, if a chick is in my nest, it is my offspring. While simplistic, such cues do typically correlate reliably with relatedness, since altricial young are obviously confined to their location. As the young develop and become more mobile, the parents may switch to more biologically based recognition mechanisms. Nonetheless, this method arguably lacks sophistication and exposes the parents to the risk of brood parasitism (Beecher et al. 1981a, b; Hoogland 1995).

Recognition of kin through the existence of so-called recognition alleles is complex but plausible, at least in theory. For example, the green-beard effect proposed by Dawkins (Hamilton 1964; Dawkins 1976) describes how a given allele could mediate the expression of a specific phenotypic cue, likely some label to aid recognition, as well as the ability to detect that cue and to behave preferentially towards others who carry that cue. In practice, it can be hard to discriminate between recognition via this mechanism and recognition via phenotype matching, which has the virtue of being more parsimonious. Nonetheless, some support for the green-beard effect, or something similar, has been reported in fire ants (*Solenopsis invicta*), where individuals that are homozygous at the GP-9 locus in the ant genome are recognised and killed by ants that are heterozygous at that locus (Grafen 1998; Keller and Ross 1998). Other potential examples have been described in side-blotched lizards (*Uta stansburiana*) (Sinervo et al. 2006) and sperm cooperation in wood mice (*Apodemus sylvaticus*) (Moore et al. 2002).

Phenotype matching is a more widely invoked mechanism of social recognition. In relation to this, animals either develop a recognition template at some early labile developmental stage, based on interactions with nest mates and parents, or, alternatively, use their own cues to provide a point of comparison, sometimes called self-referent phenotype matching (Holmes and Sherman 1982; Hesse et al. 2012). By learning the phenotype of relatives in early life, an animal can later assess the phenotypic cues of unfamiliar individuals to categorise them as conspecifics or heterospecifics and further to categorise conspecifics as relatives or as non-kin.

Studies of the formation of the recognition template involved in phenotype matching have been made using the zebrafish (*Danio rerio*). Gerlach and Lysiak (2006) showed that zebrafish are able to recognise related individuals on the basis of phenotype matching. Subsequently, Gerlach et al. (2008) reported that the recognition template for kin in zebrafish is formed on the sixth day following fertilisation. Until this point, the developing young are unable to swim freely. Beyond this sixth day of their lives, the fry begin to disperse as they develop the ability to move and forage independently. The study went further by excluding self-referent phenotype matching in the larvae, since it was shown that the isolated larvae did not imprint on their own cues. Possibly the most fascinating aspect of Gerlach et al.'s study is that the larvae failed to imprint on non-kin, which may suggest a mechanism to restrict the likelihood of errors during the formation of this kin recognition template, possibly a genetic predisposition for, and sensitivity to, the chemical cues of kin. The apparent sophistication of the zebrafish template may reflect the likelihood of encountering non-kin at an early developmental stage: zebrafish scatter their eggs, so while eggs in a given locality may indeed be kin, there is a high probability that unrelated eggs will be developing nearby. Belding's ground squirrels (*Urocitellus beldingi*) also use chemical cues in the development of a recognition template. Mateo (2009) demonstrated that the squirrels were capable of incorporating the experimentally introduced odours of a 'foreign' non-kin adult female into their developing recognition template and later treated animals bearing these foreign chemical cues similarly to their own kin.

The specificity and robustness of template formation in zebrafish stands in contrast to the process in many other animals, where a greater reliance is placed on learning as a precursor to the expression of phenotype matching. In a study on live-bearing fish, Warburton and Lees (1996) raised juvenile guppies (*Poecilia reticulata*) with young of the closely related swordtail (*Xiphophorus helleri*). Guppies raised in this way displayed a preference for associating with swordtails in preference to their own species, which is the more typical pattern among guppies. Similar examples can be provided by birds, which are known to imprint sexually as well as socially based on early life experience, which presents challenges for endeavours as disparate as conservation and falconry (Bateson 1978a, b; Clayton 1990). The formation of the template involved in social recognition and acoustic communication in zebra finches (*Taeniopygia guttata*) is based on exposure to conspecific adults in early life, and deprivation of this experience affects the ability of the animals to perceive as well as to produce conspecific calls in later life (Sturdy et al. 2001; Campbell and Hauber 2009).

Self-referent phenotype matching occurs where animals use their own cues to provide a template against which to compare others (Mateo 2010). An advantage to this is its simplicity (Weddle et al. 2013). Much research on vertebrate subjects has focussed on the recognition of kin via chemical cues. Genotypic effects on the chemical signatures of individuals have long been suggested as a means by which animals could recognise kin. Particular attention has been paid to the role of the major histocompatibility complex (MHC) in facilitating kin recognition among vertebrates (Penn and Potts 1998). The MHC is a highly diverse area of the vertebrate genome involved in immunocompetence; however, the importance of the MHC in the context of social recognition is that it is thought to influence the chemical cues produced by an organism. This in turn potentially allows discrimination of conspecifics and, in particular, the identification of genetically similar individuals.

Receivers of these cues are able to reference their own cues and use these to provide a template against which to compare the cues of the sender – the more similar the chemical cues of the sender are to its own, the more closely related that individual is likely to be. Recent research has emphasised the possibility of recognition via a broader repertoire of chemical cues relating more generally to the genome of an organism, rather than specifically to the MHC in particular (Sturm et al. 2013; Overath et al. 2014). An appealing aspect of this new perspective is that it allows for a mechanism of recognition via genotype-related chemical cues that is universal to all animals and not simply to vertebrates.

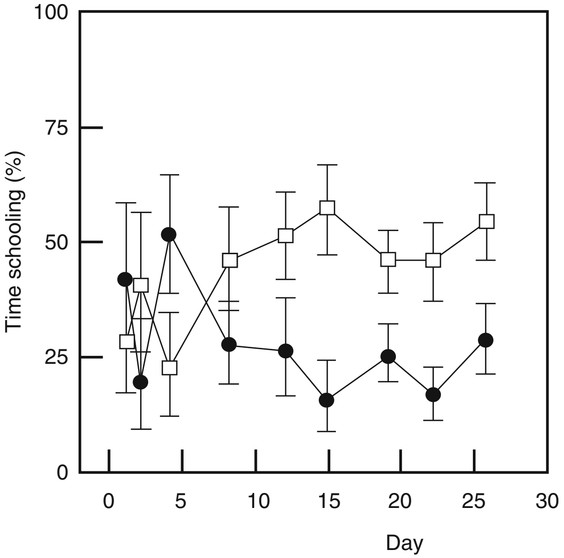
Self-referent phenotype matching is not restricted to the recognition of kin, however. Weddle et al. (2013) demonstrated the use of this approach in the identification of previous mates in decorated crickets (*Gryllodes sigillatus*). Fish are also known to use self-referencing in social association decisions. Three-spined sticklebacks (*Gasterosteus aculeatus*) prefer to associate with unrelated conspecifics that have had a similar recent diet as themselves or that have occupied water with a similar chemical profile (Ward et al. 2004a, 2005). Cues pertaining to recent habitat and diet experience also mediate association decisions in ants, prawns and other fish – typically, receivers prefer to associate with senders that express cues similar to their own. The functional explanation for this preference is not yet understood, but it could potentially allow a means of navigating within the social environment, stabilising social interactions and possibly even facilitating the sharing of relevant local information.

Finally, the cues used in recognition may be learned on the basis of social experience. Learned cues form the basis of individual recognition; however, it is worth pointing out that true individual recognition need not be the inevitable outcome of such learning. Learned cues could just as well be involved in a more general, class-level form of recognition, whereby some generic identity is accorded by the receiver in response to the sender's cues. Research undertaken by Griffiths and Magurran (1997a) on the guppy (*Poecilia reticulata*) neatly demonstrated the importance of a learning period for the fish to acquire the recognition template through repeated interactions. The ability to recognise familiars developed over a period of 12 days (see Fig. 2.2).

2.5 The Sensory Bases of Sociality

There is considerable variation among taxa in relation to the cues that are used in social recognition. Much research has primarily focussed upon acoustic cues (Beer 1970; Falls et al. 1982; Beecher 1989; Beecher et al. 1989; Insley 2000; Insley et al. 2003), chemical cues (Halpin 1980; Duvall 1986; Johnston 2003), visual cues (Tibbetts 2002; Detto et al. 2006) and others, including electric cues (Stoddard et al. 1996). The simultaneous use of multiple types of sensory cue provides receivers with a means of cross-referencing the information that they obtain and therefore decreasing the likelihood of errors (Uetz and Roberts 2002; Partan and Marler 1999; Rybak et al. 2002).

Fig. 2.2 Griffiths and Magurran (1997a) measured the mean percentage time spent by a female guppy in the presence of familiar (*open squares*) and unfamiliar (*solid circles*) over a period of time. Gradually, a preference for familiar individuals emerges as the fish begin to recognise familiars



Acoustic cues play a key role in social recognition in many animals, including mammals, birds, amphibians, insects and even fish. An advantage of acoustic communication is that, in the right circumstances, it has a range that far exceeds that of visual cues. This might be of particular relevance in maintaining and coordinating social ties across long distances or in complex environments. Spehar and DiFiore's (2013) study on spider monkeys (*Ateles* spp.) emphasised the role of loud calls among dispersed groups in precisely this way. In addition, acoustic calls can be used to identify the caller, certainly in mammals and birds (Wanker et al. 1998; Frommolt et al. 2003). A study on the range of contact calls in African elephants, *Loxodonta africana*, demonstrated the ability of the animals to recognise the call of another specific individual at distances of up to 2.5 km. Generally, however, individual-specific elements of the calls begin to be lost at distances of over 1.5 km (McComb et al. 2003).

Remarkable levels of specificity can be achieved by receivers using acoustic cues. Two obvious examples of this are the ability of penguins to locate and identify their own offspring in the crowded and often cacophonous conditions of the rookery by acoustic cues alone (Robisson et al. 1993; Jouventin et al. 1999). Dolphins produce signature whistles, calls that encode their own identity and which are used by receivers to enable individual recognition and also to promote group cohesion (Sayigh et al. 1999; Janik et al. 2006). In contrast to other animals whose calls contain individual elements, but where the individuality is primarily a by-product of anatomical or physiological differences, bottlenose dolphins (*Tursiops truncatus*) encode their individuality by modulating the frequency of their whistles (Kershenbaum et al. 2013).

While acoustic cues may enable individual recognition in some species, in others they may facilitate a more general form of recognition. For example, Wilkinson and Boughman (1998) reported that greater spear-nosed bats (*Phyllostomus hastatus*) call at the outset of foraging trips, possibly to first establish and then maintain social groups over the course of the trip. But while the calls of bats from the same roosts converge to form a group-specific call ID, there is no evidence that the calls facilitate individual recognition (Boughman and Wilkinson 1998). In a study encompassing 16 different European bat species, Pfalzer and Kusch (2003) were able to identify species-specific acoustic elements and further suggested the possibility that there was enough difference between individuals' calls to enable individual recognition. Similarly, male stripe-backed wrens, *Campylorhynchus nuchalis*, are able to recognise and distinguish between members of their own group and members of other groups and also between their own patriline and others on the basis of learned group-specific calls (Price 1999; Wiley and Wiley 1977).

Although humans are poorly adapted to detect and decipher chemical cues, countless animals depend on these cues for social recognition. Much valuable research on this topic has been conducted on recognition via the chemical composition of the cuticle in insects (Singer 1998). The chemical profile of hydrocarbons in the cuticle allows an insect to discriminate according to the species, sex and relatedness of another individual and, for social insects, allows them to discriminate whether another individual is from the same colony, whether it is an adult or a larva and what caste it belongs to (Gamboa et al. 1986; Singer 1998; Cotoneschi et al. 2007). The chemical signature of each individual has both genetic and environmental components and may be homogenised to an extent by the frequent interactions that occur between colony members either through indirect contact or through mutual grooming and trophallaxis (van Zweden and D'Ettorre 2010). Cuticular hydrocarbons are also implicated in recognition between other insects, including cockroaches, *Blattella germanica*, and spiders, *Stegodyphus lineatus*, which are capable of recognising unfamiliar kin using these cues (Lihoreau and Rivault 2009; Grinsted et al. 2011).

Individual recognition on the basis of chemical cues is a feature of the social organisation of species including Belding's ground squirrel, As is the case with many other mammals, variable chemical cues are produced at a number of sites on the animal's body (Johnston 2003). Interestingly, each individual is able to build a chemical profile of another squirrel and is able to combine and generalise different chemical cues from the same individual which may increase the precision with which individuals can be discriminated and likely also transmits information about its physiological state and recent activity (Mateo 2006). Similarly, ring-tailed lemurs (*Lemur catta*) are capable of individual recognition on the basis of odour cues alone, furthermore, the scent produced by each individual contains information on its age, reproductive status and rank (Palagi and Dapporto 2006).

Australian gidgee skinks (*Egernia stokesii*) are able to distinguish between unrelated members of their own social group and unrelated, unfamiliar individuals based on chemical cues, suggesting that they recognise some group-specific label relating to the environment or that they are capable of learned individual recognition. Fish and amphibians make extensive use of chemical cues for social recognition. Juvenile coho salmon are attracted to cues of members of their own population (Courtenay et al. 1997), while other salmonids use chemical cues to facilitate kin recognition (Moore et al. 1994; Olsen et al. 1998). While such cues are typically expressed in urine, or faeces, the protective mucus which coats the skin of fish can also yield chemical cues that are important in social recognition. Matsumura and co-workers' (2004) study on marine striped catfish (*Plotosus lineatus*) identified a phosphatidylcholine molecular species in the fish's mucus that is used in familiar group recognition.

Chemical cues are unlike other recognition cues in that they persist to an extent over time. For this reason, many animals tend to use them to advertise their presence in the environment by so-called scent marking. The act of scent marking has the effect of stabilising the social interactions of group-living mammal species, such as hyenas and wolves, by marking out their range or territory. Information about the sender is encoded by the presence of both volatile and non-volatile chemicals. Volatile chemicals are particularly valuable in terms of increasing the range over which the cues can be detected; however, while increased volatility improves the radius of the signal, it also decreases its longevity. The decay of volatile cues provides the receiver with some amount of temporal information about the cue. The sender provides most of the content of these chemical cues, passing on information about, for example, its physiological and reproductive state. In addition to this, recent research has highlighted the role of microbes that inhabit the scent glands of the animals in mediating their chemical cues, potentially contributing to unique individual or group-specific elements in the cues (Drea et al. 2002; Theis et al. 2013).

Proteins expressed in urine also represent a major source of chemical cues. Receivers are able to use these proteins in making an assessment of relatedness. Ligands derived from the MHC are present in urine, as indeed are the so-called major urinary proteins (MUPs), which comprise virtually all of the proteins in mouse (*Mus domesticus*) urine (Hurst and Beynon 2004). Both MHC ligands and MUPs encode genetic individuality to an extent; hence, both could play an important role in producing the unique chemical signature expressed by each organism, which is of such importance to receivers in chemically identifying kin and possibly the specific identity of the sender (Overath et al. 2014; Sturm et al. 2013). Considerable study has been made of the role of the MHC in promoting chemical recognition of kin in fish. Olsen et al. (2002) showed that the strength of the preference of juvenile Arctic charr (*Salvelinus alpinus*) to associate with the chemical cues of siblings was mediated by the similarity of these siblings' MHC genotypes to that of the choosing individual. Interestingly, when given a choice between the chemical cues of a sibling with a different MHC genotype to itself and a non-sibling with a similar MHC to itself, the focal fish demonstrated no clear preference, suggesting that kin recognition may be mediated by more than just MHC matching; nonetheless, the experiments do appear to demonstrate an important role for MHC-based cues in this process. Building on these findings, Rajakaruna and colleagues (2006), also working on salmonids, showed that while MHC-based cues are important in kin recognition among juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*), the fish may be able to access other chemical cues derived from other areas of the genotype in kin recognition.

Visual cues play a huge role in animal communication and in social recognition among individuals of a range of species. The ability to discriminate among conspecifics on the basis of visual cues alone is widespread in mammals (Kendrick et al. 2001), birds (Bird and Emery 2008; Ryan and Lea 1994; D'Eath and Stone 1999), reptiles (Olsson 1994; Van Dyk and Evans 2007) and fish (Balshine-Earn and Lotem 1998; Bshary et al. 2002; Grosenick et al. 2007).

The specific visual cues that are attended to during social recognition are of course dependent on the species. Humans reply primarily on facial features and characteristics for visual identification of others, and we are by no means the only species to do this. Indeed, facial recognition seems to be a general feature among primates (Leopold et al. 2005; Leopold and Rhodes 2010). Perhaps more surprisingly, a wide range of other animals are also capable of facial recognition. Sheep, cattle and pigeons are each capable of recognising and distinguishing between individual conspecifics from two-dimensional images (Watanabe and Ito 1991; Kendrick et al. 2001; Nakamura et al. 2003; Coulon et al. 2007, 2009). Among many species of birds, patterns of plumage on the face are important facilitators of social recognition (Whitfield 1987; Brown and Dooling 1992; Dale et al. 2001). Facial markings are also known to be important among invertebrates (Detto et al. 2006; Van der Velden et al. 2008). Tibbetts (2002) demonstrated the importance of facial markings as a means of signalling quality in one species of paper wasp (*Polistes dominulus*) and as a means of individual identification in another (*Polistes fuscatus*) (Sheehan and Tibbetts 2011; Tibbetts and Lindsay 2008; Tibbetts 2002; see Fig. 2.3). While facial characteristics are often important in promoting recognition, it seems reasonable that many animals examine patternings over a conspecific's entire whole body. For example, Ewer (1973) suggested that the highly individualised coat markings of wild dogs (*Lycaon pictus*) could be used for recognition, while Fricke (1973) demonstrated the importance of stripe patterns in recognition by clownfish.

While the majority of studies on the salient cues involved in social recognition have focussed on single sensory modalities, animals generally live in a multimodal world. Combining and cross-referencing information received through different channels allow animals to minimise the risk of failing to identify or of misidentifying an individual. Further, integrating the information from different senses allows the receiver to build a richer mental representation of a third party. Ring-tailed lemurs (*Lemur catta*) attend more closely to the chemical and acoustic cues of familiar individuals when these are presented in association compared to when these are mismatched across stimulus individuals, suggesting that the lemurs form multisensory representations of other individuals (Kulahci et al. 2014). Horses (*Equus caballus*) are also capable of forming multimodal representations of individuals based on cross-referencing visual and acoustic cues (Proops et al. 2009). Similarly, mosquitofish (*Gambusia holbrooki*) respond more strongly to the presentation of a combination of chemical and visual conspecific cues than to either cue type in isolation (Ward and Mehner 2010).

2.6 Recognition Beyond Identification

Many authors argue that social recognition goes beyond discrimination and categorisation of animals encountered within the environment to include the assessment of individual qualities and aspects of individuals which are not intrinsic to their identity and which can change over relatively short periods of time (Dittrich 1990; Miklosi et al. 2004). This might include determining the strength or competitive ability of another animal, whether or not it has salient information, its emotional or

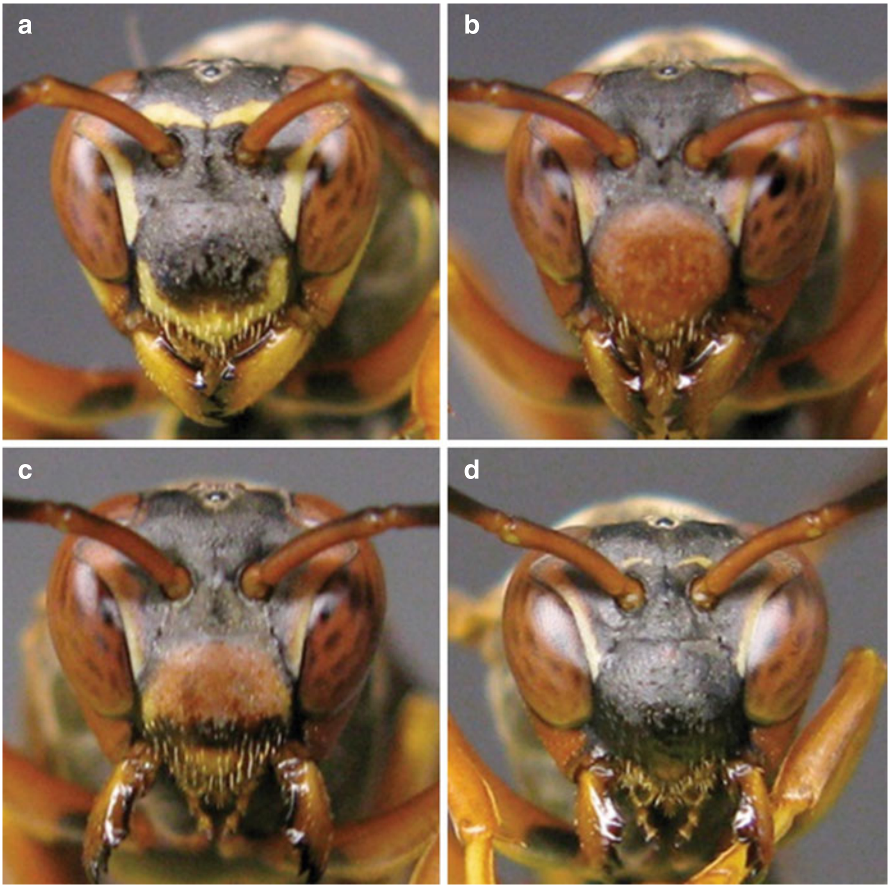


Fig. 2.3 Variation among individuals in facial patterning is used by paper wasps, *Polistes fuscatus*, to recognise one another (Sheehan and Tibbetts 2008)

motivational state and its role and participation in complex relationships. It is likely that group-living animals in particular are highly attuned to such considerations, since adopting the appropriate social behaviour in light of this information is crucial to any individual's ability to successfully navigate within its social environment.

Recognition of social rank is of considerable importance to group-living animals. The cost of fighting promotes the evolution of clear, unambiguous and honest signals relating to competitive ability, including proxies such as size and condition, as well as formalised and often ritualistic signals of dominance and, equally importantly, submission. There are different pathways to determining rank. One pathway relates to a badge or signal which communicates rank, but which is not connected with individual identity, as seen in many species of birds (Johnsen et al. 1996; Eens et al. 2000; Mennill et al. 2003; Bokony et al. 2006) and in the facial patterns of some species of paper wasps (Tibbetts and Lindsay 2008). Another, more complex approach is to associate an individual identity with dominance information, as occurs in Chacma baboons (*Papio ursinus*) (Bergman et al. 2003). The association of identity and information about an individual has also been reported in contests among crustaceans. Karavanich and Atema (1998) reported the ability of lobsters (*Homarus americanus*) to remember the identity of previous combatants and the outcome of their contest. Similar results have also been reported in crayfish (*Cherax destructor*) (Van der Velden et al. 2008) and hermit crabs (*Pagurus longicarpus*) (Gherardi et al. 2005). The interesting aspect here is that while losing lobsters will retreat from their earlier conquerors, they do not retreat from dominant individuals whom they have yet to fight, suggesting the absence of general dominance cues. Males of the cichlid fish, *Astatotilapia burtoni*, are known to be capable of inferring the competitive ability of other males, based on observation of contests. They can then use this information in association with the identification of individual combatants to adjust their behaviour accordingly (Grosenick et al. 2007). In a grouping context, minnows (*Phoxinus phoxinus*) are able to distinguish among conspecifics on the basis of their competitive ability and to preferentially associate with relatively less competitively able individuals, even in the absence of direct cues such as feeding rate or aggressiveness (Metcalfe and Thomson 1995).

Determining another animal's emotional or motivational state is also vitally important to the formation and maintenance of social relationships and to the functioning of social groups of many species. Often it is beneficial for the sender to communicate its emotional state unambiguously via posture, colouration or facial expression; however, information may also be communicated without intent. For example, macaques can acquire a fear of objects such as replica snakes by watching the facial expressions and bodily postures of conspecifics as they interact with these objects (Cook and Mineka 1989). Sheep are able to recognise the emotional state of conspecifics simply from photographic images and prefer those with calm expressions over those displaying facial signs of distress (da Costa et al. 2004; Tate et al. 2006). It seems likely that the eyes are the key component of the signal, and in particular the amount of eye white displayed correlates with stress levels (Tate et al. 2006; Sandem et al. 2006). Cephalopods are able to communicate a wide range of emotional states through rapid and complex colour changes across the surface of their bodies (Hanlon and Messenger 1988; Adamo and Hanlon 1996), while agitated shoaling fish are known to flick, or wave, their fins possibly as a means of social communication (Brown et al. 1999).

2.7 Summary

Social recognition provides the foundation for the social organisation of populations and species. However, the formation of animal groups, including some of the largest social aggregations, often does not require a high degree of sophistication in terms of recognition mechanisms and capabilities. Basic social attraction towards conspecifics, allied to commonalities in habitat and resource preferences, is sufficient to explain the ways in which animals like krill or pelagic fish coalesce into groups. Beyond this, considerable strides have been taken in recent years to provide us with some understanding of the forces governing the interactions between individual animals in the formation and maintenance of social aggregations, and we examine this topic in detail in the next chapter. But while complex recognition is not a prerequisite of animal grouping behaviour, increasing specificity of recognition mechanisms allows for the development of greater intricacy in social interactions, in turn structuring and shaping patterns of association among individuals. This in turn leads to social phenomena such as kin- or familiar-structured groups. Although such patterns have been recorded in a variety of animal taxa, work remains to be done if we are to fully understand the underlying recognition mechanisms in many cases. For example, familiarity is important in shaping the social interactions of many animal species, yet what we actually mean by familiarity varies considerably across taxa and contexts. In some cases, it may require individual recognition, in others, or the recognition of some basic group-specific label. The difference is an important one, since the difference between them is likely to have considerable implications for our understanding of the social dynamics of the species in question. Hence, approaches that meld both the functional considerations of observed patterns of social organisation, with a clear understanding of the mechanisms of social recognition, are likely to be best placed to advance our understanding of social interactions.

Attraction, Alignment and Repulsion: How Groups Form and How They Function

3

3.1 Introduction

Aggregations of animals provide arguably the most dramatic sights in the natural world. One reason for this is their scale: some animal aggregations can be truly huge. Krill swarms can be visible from space, vast shoals of fish that measure kilometres in length and dense, wheeling clouds of starlings so enormous that they seem to obliterate the sun. But beyond scale, an additional factor contributing to the spectacle is the sense in which the many individual animals appear to be acting with unanimity of purpose. The observer is first transfixed by the sight and then questions occur: Why have they gathered here in such numbers? How do the animals behave in such a coordinated way? Our understanding of the first question is reasonably well developed and there is a rich literature concerned with the means by which animals are socially attracted to one another and subsequently coalesce into groups. Answers to the second question have proven much more difficult to find, although the question has caught the imagination of naturalists and scientists alike for centuries. Somehow, the individuals in the group seem to act in unison. They turn together, they flow around obstacles, and they move as one. Their coordination is amazing – as though some centralised controller dictates all movement. Until relatively recently – midway through the twentieth century – it was an established idea that group members were capable of some form of collective telepathy, or 'thought transference', allowing each to coordinate its actions with the collective or to follow leadership initiatives. But while this idea has some appeal, it is an illusion. Recent years have seen breakthroughs in our understanding of how repeated interactions between animals can produce the observed patterns. This chapter examines the current state of our knowledge on the mechanisms underlying social aggregations and collective behaviour.

A. Ward, M. Webster, *Sociality: The Behaviour of Group-Living Animals*,
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3.2 Finding Conspecifics and Forming Groups

For members of social species, the drive to locate and associate with conspecifics is strong. In isolation, individuals manifest a cascade of physiological and behavioural changes, often relating to stress, and among species that are strongly social, this stress may be considerable. Isolated Japanese quail (*Coturnix japonica*) that have been selected either for low or for high levels of sociality produce distress calls. The latency to make these calls and the frequency with which they make them relates directly to their social tendency with highly social individuals producing more calls (Launay et al. 1991). This pattern of producing alarm calls when separated from a group appears to be common among social birds and mammals (Gaioni and Ross 1982; Lingle et al. 2012). Mills and Faure (1990) resorted to the somewhat unusual expedient of measuring the motivation of Phsianid chicks to associate with conspecifics by rewarding them with social time in return for performing the task of walking on a treadmill. In a similar way, the sight of conspecific images activates the dopaminergic 'reward' pathway in zebrafish, demonstrating a fascinating mechanism underlying the motivation of animals to form associations (Saif et al. 2013).

Groups may break up and reform over different time spans. In fission-fusion societies, the ability to relocate conspecifics following the separation of the group into subgroups is fundamental to that species' social system. Fission may occur in response to environmental conditions, for example the onset of night, such as occurs among shoals of some species of fish break up each evening and reform in the morning as it gets lighter (Pavlov and Kasumyan 2000). Fission may also occur in response to changes in resource distributions (Wittemyer et al. 2005; Henzi et al. 2009) or in response to a predator threat or direct attack, causing the group to splinter and temporarily isolating a proportion of group members (Handegard et al. 2012). Additionally, the strength of social attraction may change across a longer time span, as is the case among western black widow spiders (*Latrodectus hesperus*), which form groups of up to eight individuals in autumn and winter but are solitary during the spring or summer months (Armstrong and Whitehouse 1977). In any case, the initial process of aggregation or later reaggregation occurs through social attraction between individuals via the detection of sensory cues in the environment.

Studies of the response of individuals towards conspecific cues have been made in a wide range of social species and examining a variety of sensory cues. Fish are particularly amenable to manipulative laboratory studies in this context. Shoaling species are strongly attracted to visual cues of conspecifics and to chemical cues. Many laboratory tests have been conducted using a binary-choice approach, whereby a focal fish is presented with a shoal of conspecifics at one end of an aquarium and some alternative at the other end, such as a shoal of conspecifics of a different phenotype or size, a shoal of heterospecifics or no shoal at all. Typically, shoaling fish approach and remain in close proximity to the side on which the conspecific cues are presented. Keenleyside (1955) demonstrated that fish given access either to the visual cues or to the chemical cues of conspecifics use these to locate and remain in proximity to those conspecifics. A similar approach has been used to examine social tendencies in many fish species, both within and between species, as well as amphibian larvae. Evans et al. (2007) studied aggregation behaviour in two species of decapod crustacean; one of these, the brown shrimp (*Crangon crangon*) is not naturally found in groups, and the other, the common prawn (*Palaemon elegans*) is. Using the binary-choice approach, the authors found evidence of social attraction in the prawn, but not in the shrimp, suggesting social attraction as the means by which aggregations form in these species. The binary-choice approach has also been adapted for use with mammals, such as with Michelena et al.'s (2005) study of sheep (*Ovis aries*), which again revealed strong evidence of social attraction but also evidence for sex-biased social attraction between peer males which relates to social segregation of the sexes in free-ranging flocks.

The binary-choice approach can also be used to make fine-scale manipulations of aspects of the cues available to a choosing animal in order to determine precisely what component of an overall cue is attractive. A study by Ward et al. (2002a) examined how fish weighted visual and chemical cues in two sympatric cyprinid species. By juxtaposing the cues available to a single choosing fish in a binary-choice test, Ward and coworkers were able to present fish with a choice of conspecific visual cues in association with heterospecific chemical cues versus heterospecific visual cues in association with conspecific chemical cues. The fish elected to associate with the shoal that seemed to express conspecific chemical cues, even though the visual cues were those of heterospecifics, demonstrating the primary importance of chemical cues in social attraction in these species.

Colonially nesting birds, including many species that do not typically live in groups outside of the breeding season, often display strong social attraction towards groups of conspecifics once they feel the urge to nest. Storm petrels (*Oceanodroma* spp.) are attracted to the vocalisations of conspecifics and to the odours of conspecifics when locating suitable nesting habitats (Buxton and Jones 2012). Similarly, the least flycatcher (*Empidonax minimus*), though territorial for most of the year, shows strong evidence of social attraction when locating a nest site (Fletcher 2009). In these and similar cases, these largely solitary birds appear to be using conspecific presence as public information on the suitability of a nest site, as well as joining a nesting aggregation to obtain some measure of protection from brood predators. Some species of communally roosting bats forage independently but associate with conspecifics during daily resting periods. Where roosting sites are ephemeral, conspecifics must be located and auditory signals are known to play an important role in this process. Furmankiewicz et al. (2011) demonstrated the attraction of noctules (*Nyctalus noctula*) to the playbacks of social calls, even observing the bats to land on loudspeakers, indicating the role of calls in broadcasting the location of the roost. The calls of bats in this context may be more than simply a passive means of locating conspecifics. In a study of Spix's disc-winged bat (*Thyroptera tricolor*), Chaverri et al. (2010) reported that flying individuals made what the researchers termed 'inquiry calls' which drew a rapid 'response call' from bats in the roost. These calls may indicate attempts at active recruitment to the roost.

The extent to which an individual is attracted to a group of conspecifics is dependent upon the size of the group – larger groups typically exert a more powerful socially attractive force on an individual. This phenomenon is seen in the location of colonial nesting grounds by birds, where a greater number of established nests may be taken as a reliable source of social information on the quality of the local resources. As a general rule, larger nesting colonies tend to promote the survival and lifetime reproductive success of colony members (Serrano et al. 2004, 2005; see also Chaps. 6 and 7). Exclusion from the largest colonies seems to act as a brake on the perpetual growth of colonies. Fish given the choice of associating with two shoals will preferentially associate with the larger of the two alternatives, and the strength of the preference relates to the magnitude of the difference in size between the two shoals (Hager and Helfman 1991; Pavlov and Kasumyan 2000). Taken together with the finding that smaller, more vulnerable fish tend to show a stronger preference for larger shoals than do larger conspecifics, this suggests that the selection of larger shoals relates to the greater anti-predator protection afforded by such groups. Breder (1951) likened the attractive force generated by larger animal groups to the gravitational pull of massive objects and suggested that the attractive forces could effectively generate a distribution of multiple dense groups (what Breder referred to as ‘clots’) of animals. In support of this conjecture, Breder cited experimental work on redfin (*Tribolodon hakonensis*) in which it was shown that large groups are more attractive than small and that the strength of the attraction decreases with distance from the group. Building on this, Niwa (2004) published a simple ‘merge and split’ model in which groups moved at random throughout their environment. Whenever two groups met, they merged, while groups were programmed to split periodically. This approach, though simple, manages to replicate, with surprising accuracy, the distribution of group sizes in free-ranging fish. Many other factors influence the extent to which an individual is socially attracted towards conspecifics, including the tendency to size-match, the risk of transmissible disease and parasitism and the behaviour of those individuals.

3.3 Collective Behaviour

Once a social aggregation is formed, the members of that aggregation may be seen to coordinate their actions and to behave in a way that suggests unanimity of purpose across the individuals in the group. This is the basis of collective behaviour, which examines how repeated local interactions between individuals can produce group-level, so-called global, patterns. Understanding how different components interact to form a system in a manner which is synergistic and often difficult to predict in advance is an important goal across a range of different disciplines. The study of collective behaviour provides insights not only into the dynamics of social groups as described here but also has applications in fields including developmental biology, immunology and neurology. Beyond biology, collective behaviour is also of considerable interest in disciplines such as sociology, economics and indeed any research field concerned with complex systems.

3.3.1 Interactions in the Group and Social Forces

How do individuals behave collectively? How do they coordinate and synchronise their actions? To understand these questions requires an appreciation of the dynamics of the interactions between individuals within the group. One of the earliest scientific considerations of this topic was provided by Albert Parr (1927) who speculated that shoaling fish effectively balance two competing forces, those of attraction and repulsion to conspecifics. Elaborating on this, Breder (1954) described forces of repulsion and attraction and proposed ways in which the two forces could act variably according to the distance between individuals: too much space between them and they tend to move together; too little and they move apart. The appeal of this approach can be found in its intuitive simplicity. Moreover, it is lent credence by data from real animal aggregations. The idea that animals should adjust their distance to other individuals in the group to balance forces of attraction and repulsion produces the key prediction that there should be a distribution of nearest-neighbour distances (NNDs) with a clear peak, representing in some way the ideal spacing for a given species under a given set of conditions. Many studies have reported such data across a range of social species, and the congruence in typical NNDs across taxa is interesting (see Table 3.1)

Nearest-neighbour differences are also context-dependent and can be affected by both biotic and abiotic factors. For example, many schooling fish species only form these cohesive groups during the day. At night, the fish tend to increase their NNDs, in some cases causing dissolution of the groups (Aoki and Inagaki 1988; Emery 1973; Smith et al 1993). This may reflect the fact that the anti-predator function of schooling operates primarily to confuse predators that are reliant on their visual sense for hunting (Krakauer 1995; see Chap. 4). A mechanistic explanation for the same pattern might argue that the low light levels at night make it difficult or impossible to gather the visual information required for shoaling (Pavlov and Kasumyan 2000). But while blind fish do have greater NNDs than sighted shoal mates, they are nonetheless capable of cohesive shoaling (Partridge and Pitcher 1980; Pitcher et al. 1976). Light intensity also affects the grouping behaviour of crustaceans such as krill (*Euphausia superba*) and the mysid, *Paramesopodopsis rufa*. Both species

Table 3.1 Reported nearest-neighbour distances (NNDs) for a range of species

Species	NND (body lengths)	Reference
Coullana canadensis (subclass Copepoda)	1–2	Yen and Bundock (1997)
Harlequin fly/midge (*Chironomus riparius*)	1–2	Kelley and Ouellette (2013)
Krill sp (*Nyctiphanes australis*)	3	O'Brien (1989)
Blacksmith (*Chromis punctipinnis*)	2	Parrish and Turchin (1997)
Cod (*Gadus morhua*) and herring (*Clupea harengus*)	≈2.2	Pavlov and Kasumyan (2000)
Sheep (*Ovis aries*)	<2	Michelena et al. (2008)
Buffalo (*Syncerus caffer*)	2	Prins (1996)

increase their nearest-neighbour distances as light intensity increases. The author of this study argues that if spacing behaviour is visually mediated, the increased NNDs may be a reflection of the improved visual capabilities of the animals as light intensity increases (O'Brien 1989).

An underlying assumption is that the NND reflects the functional requirement that the animals are close enough to benefit from the protection afforded by group living and to enable efficient information transfer among individuals yet far enough apart that locomotion and escape behaviour are not hindered. Under predation threat, animals across a range of taxa tend to reduce their nearest-neighbour distances, in line with Hamilton's (1971) selfish herd predictions, discussed later in this book (Hurley 1977; Major 1977; Viscido and Wethey 2002). In terms of locomotion, birds on the ground, or on water, maintain lower NNDs than birds in flight. Surf scoters (*Melanitta perspicillata*) in a swimming flock had an NND of around 1.5 body lengths (Lukeman et al. 2010), while Canada geese (*Branta canadensis*) in flight have an NND (from the centre of each bird) of between 4 and 5 body lengths and flying starlings (*Sturnus vulgaris*) in flocks maintain an NND of between around 3 and 7 body lengths (Ballerini et al. 2008; Major and Dill 1978).

In addition to adjusting their behaviour through forces of attraction and repulsion to maintain preferred NNDs in a group, it has been assumed that the kind of coordinated and polarised behaviour seen in groups must result from individuals aligning with near neighbours. In other words, it was predicted that animals will tend to show allelomimetic behaviour, whereby they conform their own speed and direction of travel to that of near neighbours. Partridge (1981) was able to show that pollock (*Pollachius virens*) closely matched their behaviour to two near neighbours. At the group level, this increases the level of polarisation, while at the individual level, it facilitates not only the basic regulation of distances between animals but also the transmission of social information (Partridge 1982).

These simple heuristics – attraction, repulsion and alignment – sometimes referred to as the rules of interaction, provide the framework which is still in common use today when we consider the mechanics of collective behaviour (see Fig. 3.1). Attraction is a prerequisite for the formation of social aggregations, repulsion restricts crowding and prevents collisions and alignment is proposed to produce coordinated motion. These rules have been the basis of simulation models that seek to examine emergent group-level patterns by encoding behaviour in individuals. Self-propelled particle models have been at the forefront of this work (Okubo 1986; Vicsek et al. 1995; Czirok and Vicsek 2000). In these models, multiple particles move in 1, 2 or 3 dimensions. Depending on the model, each particle is surrounded by a series of concentric zones featuring an inner repulsion zone, an intermediate alignment zone and finally an outer attraction zone (Huth and Wissel 1992). Typically, each particle moves continuously, adjusting its speed and direction depending on its interactions with other particles. In particular, each particle will move away from particles in its repulsion zone, move towards particles in its attraction zone and adjust its orientation to align with those in its alignment zone (Aoki 1982; Gueron et al. 1996; Helbing and Molnar 1995; Okubo 1986; Reynolds 1987; Romey 1996).

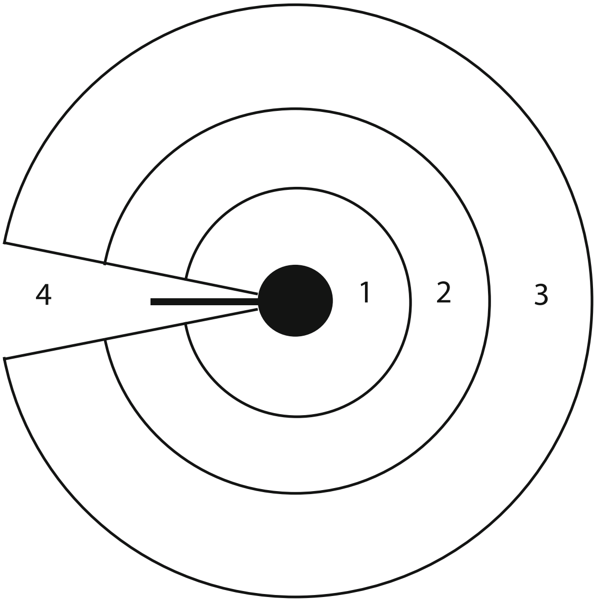

Fig. 3.1 Schematic describing the zonal rules applied by an individual to their interactions with others. Three zones are suggested, ranging outward from the focal individual at the centre are (*1*) the zone of repulsion, (*2*) the zone of orientation and (*3*) the zone of attraction. An area (*4*) directly behind the animal is sometimes referred to as the blind angle

The Boids ('bird-oid object') programme developed by Craig Reynolds was the first to simulate the movement of multiple animals in three-dimensional space. In its simplest form, it uses basic rules, such as collision avoidance, alignment and attraction to the centre of the group, and in doing so is able to replicate key aspects of the behaviour of real-life animal groups. This and similar approaches in subsequent years led to considerable refinement and significant progress towards the goal of understanding the dynamics of collective behaviour (Czirok et al. 1999; Huth and Wissel 1992; Flierl et al. 1999; Reuter and Breckling 1994; Gueron et al. 1996; Levin 1997; Romey 1996). Building on these, and on Aoki (1982), Couzin et al. (2002) produced a detailed model of a three-dimensional group in which individuals were subject to the local behavioural rules of repulsion, alignment and attraction. The rules were prioritised so that the primary response was to maintain a minimum distance between individuals and thus avoid collisions; if individuals were not engaged in avoidance behaviour, then they would be attracted to distant individuals (within their range of perception) and to align with near neighbours. In addition, each had a blind angle corresponding to the segment of an animal's visual field directly behind that it cannot see; hence, it ignores individuals within this segment. Finally, an error term introduces an element of noise to the model, corresponding with environmental stochasticity and with the errors made by individuals in collecting and responding accurately to information. The cumulative effect of these parameters was to produce realistic group behaviour in particles – virtual animals – but importantly also to show that a collective system could transition between different states according to relatively small changes in the characteristics of local interactions and we discuss this in greater detail later in this chapter. Transitions in group behaviour were also reported by Vicsek et al. (1995), in particular the tendency of order to emerge from disorder in animal groups. Unlike Couzin et al.'s (2002) model, that used by Vicsek et al. includes only the rule that particles should align with nearby individuals, plus random perturbations of the system, or noise. As the density of particle increases to meet a threshold, a phase transition occurs: the level of alignment among the particles in the system switches from low to high and hence order emerges from the disorder.

The simulation models presented by researchers such as Viscek et al., Romey and Couzin et al. provide a neat demonstration of how simple rules encoded at the individual level can induce fascinating group-level patterns. Moreover, they show how collective phenomena can result from different rules – in Viscek et al. model an alignment term, plus noise; in Couzin's model, attraction, repulsion, alignment, a blind angle and noise; and in Romey's model, attraction and repulsion in concert with variability among individuals (Romey 1996). Indeed, Deutsch et al. (2012) contended that in any unitary system comprising individuals that are similar, that move at a steady speed, that interact with others over a given range by changing direction and which are susceptible to noise, collective motion is almost certain to result. Perhaps it is unsurprising then that many different models have been proposed, each of which is capable of reproducing real-world patterns. In some cases, this may relate to specific qualities of the system that a simulation model seeks to explore, for example, Jeanson et al.'s (2005) model of cockroach aggregation, which uses a highly localised attraction, corresponding to the actual means of recognition and attraction in cockroaches, through antennal contact. This attraction-only model reproduced the patterns of aggregation seen in the cockroaches. Couzin and Franks (2003) modelled the behaviour of army ants (*Eciton burchellii*) in trails using a variant of the repulsion zone, based on the local perception radius. Ants approached too closely would turn, or reduce speed, where possible. Rather than using attraction to conspecifics, or alignment zones, as a rule for motion, the ants navigate according to chemical cues provided by a pheromone trail (Evershed et al. 1982). The model demonstrates a coordinated collective response based on these individual rules and accurately replicates the formation of traffic lanes, as seen in foraging army ants in the wild.

While attraction/repulsion/alignment models have been able to capture key aspects of the behaviour of groups, including phase transitions, researchers have also been able to reproduce elements of collective behaviour with simplified models. For example, Strömbom (2011) described a model using only a local attraction term that was able to produce a diverse range of different collective patterns, especially when a blind angle was invoked, including swarms, mills and aligned, travelling groups. Perhaps more surprisingly still, inclusion of an alignment term in this model acted to inhibit the formation of certain aspects of collective behaviour within the group. Inspired by the mass migrations of locusts and Mormon crickets, in which cannibalism plays a major role in driving the forward momentum of the group (Bazazi et al. 2008; Bazazi et al. 2010; Simpson et al. 2006), Romanczuk et al. (2009) were able to demonstrate that collective motion could result purely from the tendency of individuals to escape conspecifics approaching from behind and in turn to pursue conspecifics ahead of them, terms which are in some ways analogous to repulsion and attraction, but the model again does not require an alignment term in order to generate collective dynamics. Rather than an alignment zone, Gueron et al. (1996) proposed the idea of a neutral zone, a zone between long-range attraction and short-range repulsion, functioning to increase the effectiveness of movement by preventing the need for excessively frequent acceleration and deceleration. Increasingly, the tendency of individuals within groups to align is being seen as an outcome of repulsion and attraction, rather than as an explicit behavioural rule in its own right.

Shifts in the behaviour of grouping animals occur in response to context, such as when the group comes under attack. But while these phenomena are typically observed at the level of the group, to understand how the patterns arise, we need to examine the responses at an individual level. Hoare et al. (2004) examined the behaviour of banded killifish (*Fundulus diaphanus*) in response to food odour cues and alarm cues, reporting that interindividual distances increased during foraging, causing the break-up of defined groups, and conversely that density increased when the group perceived danger. An accompanying self-propelled particle model explained the results simply in terms of a change in the radius of the interaction zone, specifically that the distance over which killifish were attracted to conspecifics increases in the presence of a predator and decreases when food is detected. Generally, as the interaction range increases, there are more individuals with which to integrate information, so the group as a whole becomes less sensitive to minor perturbations, which in turn promotes greater coordination of behaviour. Bode et al. (2010) took a slightly different approach, generating conditions to manipulate levels of anxiety in sticklebacks, akin to adjusting levels of perceived threat. They found that under highly anxiogenic conditions, the fish adjusted their behaviour to synchronise more closely with other individuals within their group. This pattern could be replicated in a model simply by varying the individual's update frequency. In other words, individuals perceiving greater threat increase the rate at which they acquire information from their surroundings, particularly information about their speed and orientation of group mates, and adjust their own speed and orientation accordingly. This increase in update frequency allowed fish in the model to synchronise their behaviour more effectively, matching the observed empirical results.

The characterisation of an individual's neighbourhood of interaction, essentially a measure determining which near neighbours it is influenced by, is fundamental to determining the flow of information among individuals within a group and ultimately to determining the overall dynamics of collective behaviour. However, relatively minor differences in parameters describing this interaction neighbourhood can lead to considerable differences in the predictions of simulation models at the group level, making this the cause of some controversy. Two main methods have been at the forefront of efforts to characterise the interaction neighbourhood. First of all, metric interaction neighbourhoods assume that an individual will respond to individuals within a given distance. This approach has

Fig. 3.2 Starling murmuration (Walter Baxter [CC BY-SA 2.0 (http://creativecommons.org/licenses/by-sa/2.0)], via Wikimedia Commons)

an intuitive appeal and also corresponds with our understanding of the sensory fields of animals. Its main limitation is that as density within a group increases, an individual could theoretically be forced to attend to very large numbers of near neighbours, which it is unlikely to be capable of. Nonetheless, despite frequent criticism, metric interaction neighbourhoods do retain support, for example, in Attanasi et al.'s (2014) work on midge swarms. An alternative measure, based on topological interaction neighbourhoods, has gained favour recently. Topological interactions refer to the way in which an individual responds to a set of near neighbours, regardless of their distance (Viscido et al. 2005). This approach was impressively demonstrated by Ballerini et al. (2008) who filmed large flocks of starlings (*Sturnus vulgaris*; see Fig. 3.2) above Rome and found that individuals interacted with, on average, six or seven near neighbours. They argued that the advantage of this approach is that it is robust to sudden changes in density, such as those resulting from a predator strike, and this robustness acts to promote flock cohesion. A simulation model produced by Shang and Bouffanais (2014) provides some insight as to why this should be the case. Their model predicts that in terms of maximising the efficiency with which consensus can be achieved in collective decision-making, an individual should interact with its ten nearest neighbours.

A more recent approach to the question of interaction neighbourhoods considers the sensory information available to an individual, rather than the spatial relationship of neighbours to itself (Lemasson et al. 2009). For instance, it is possible to recreate a focal fish's visual field, by first distinguishing near from far neighbours by the angular area that each subtends on the focal fish's retina. We can then remove from the equation those fish that are occluded from the visual field by nearer neighbours. Strandberg-Peshkin et al. (2013) reconstructed the visual field of golden shiners (*Notemigonus crysoleucas*) in a shoal and then looked at the spread of information through the shoal, expressed as behavioural responses, through the shoal as a function of this visual field. They found that the network of interacting individuals based on visual information differed from those predicted by metric or topological interaction neighbourhoods. Moreover, a comparison of this visual field model against its metric and topological counterparts found that the visual field approach was more effective at explaining the observed empirical data and contributed to the more efficient spread of sensory information throughout a group than either of the alternative approaches. By constructing interaction networks based on the sensory information available to each individual within a group, it may be possible to predict more accurately the spread of information through that group. For most groups, the pattern of information spread using the sensory field approach should be less predictable than for topological or metric interaction networks but as a consequence may reveal more about the functional responses of animal groups to predator attacks and other perturbations.

Impressive advances have been made in our understanding of collective behaviour and particularly in linking individual behaviour with group-level patterns, and most of these advances have come through the use of simulation models. By manipulating individual interaction parameters, it has been possible to examine their influence at both the local and global level. The intuitive simplicity of the interaction rules and the small number of parameters that are generally included in the majority of models have raised the tantalising prospect of universality in the organising principles of the collective behaviour of many very different species. But while simulation models are capable of generating patterns of collective behaviour that appear similar in many respects to those observed in real animal groups, this in itself does not mean that the parameters encoded in such models are those used by animals. A common accusation levelled at the various approaches used to describe interaction neighbourhoods and social forces is that they are selected on the basis of their algorithmic simplicity, rather than on biological realism. A further criticism is that experimental results are often distilled down to an average of many pairwise interactions, producing a so-called mean field perspective. In many cases, models are concerned with specific systems and the parameters may be adjusted in order to make the model fit observed data, so that we arrive at a bespoke solution. While this is illuminating with respect to the system in question, it fails to provide general, cross-system predictions. Additionally, adjustments to models may be made at the collective level, effectively overriding the local interactions that produce the self-organised behaviour in the first instance. In some cases, models that incorporate very different parameters can produce similar outcomes (Eriksson et al. 2010); hence, these models make no discrimination between which parameters are sufficient to reproduce observed phenomena and which are necessary. The use of statistical approaches that explicitly compare different models in regard to observed data can be extremely useful (Mann et al. 2013; Strandburg-Peshkin et al. 2013; Romey et al. 2014); however, this alone does not represent a panacea. Advancing the field requires parallel advances in empirical and modelling approaches and the intimate connection of these such that models derive testable predictions for experiments to test and subsequently to further inform the models. Through these revolutions of the modelling cycle, we can further increase our understanding of collective systems (Sumpter et al. 2012). The quest for deeper understanding is being aided in no small part by rapidly improving technology in the form of tags, GPS and automated tracking, allowing experimentalists to identify and differentiate large numbers of individuals in order to collect high-resolution data on them (Dell et al. 2014; Perez-Escudero et al. 2014) and novel initiatives such as the adoption of network-based approaches to analyse collective behaviour (Bode et al. 2011a, b).

3.4 Self-Organisation and Emergence

The unifying theme of research into many disparate themes, including collective motion, decision-making, collective cognition and the dynamics of group membership, is the phenomenon of self-organisation (Bonabeau et al. 1997; Sendova-Franks and Franks 1999). To use Camazine et al.'s (2001) definition, self-organisation is a pattern that emerges at the group level of a system as a result of interactions between lower-level components of the system, in this case, individual animals. In the context of animal collective behaviour, these local interactions typically result in the coordination of activity at the level of the group (Heylighen 2013). In addition, there is the important caveat that each individual animal acts in response to local information and without reference to the global pattern (Camazine et al. 2001). Considerations for group-level outcomes are not encoded within individual-level rules – indeed individuals in most cases are unlikely even to be aware of group-level patterns. This means that group members have no global plan for the behaviour of the group as a whole and that control of the group is decentralised and distributed among the group members. Generally speaking, self-organised groups have a large number of group members, which limits the ability of any one individual to impose leadership on the group, although it does not preclude the possibility of subsets within the group exerting disproportionate influence on the group as a whole (Couzin et al. 2005; Conradt and Roper 2009); we return to this topic in Chap. 8.

A central feature of complex systems and the process of self-organisation is the way that group-level patterns are said to 'emerge' through multiple local interactions. This term refers to the notion that the patterns manifested by groups cannot be predicted on the basis of a full knowledge of the local interactions between individuals (Anderson 2002). Emergent phenomena are guided and shaped by processes of feedback and nonlinear dynamics. In other words, the outcome of a process is not directly proportional to its cause: we may see amplification or dampening of a reaction as it spreads between individuals within the group. Positive feedback can be described as the amplification of an initial perturbation in the system and is usually required in order to recruit group members to a course of action and thereby reinforce that action. An example of positive feedback is provided in the selection of resting sites by cockroaches (*Blatella germanica*). The presence of a single cockroach in a shelter increases the likelihood of a second cockroach pausing there, and as the number of cockroaches in a shelter increases, the shelter becomes disproportionately more attractive, resulting in the formation of large aggregations (Ame et al. 2004; Jeanson et al. 2005). Unfettered positive feedback can clearly create its own problems, especially in the case of nonlinear amplifications, which can be destructive to any process in which it plays a role. As a result, negative feedback may often be required to counterbalance and stabilise positive feedback cycles. In some cases, the negative feedback may be engineered by signalling, for example, in the stop signals provided by honey bees to at least partially counteract the positive feedback to the waggle dance and to limit the recruitment of hive members to a particular foraging site (Nieh 2010). More generally, negative feedback may be the result of more passive factors, such as limitations on resources, restrictions in the availability of recruits or habituation to a novel stimulus.

Conformity to an existing pattern of behaviour can stifle innovation such that, as conditions change, a group may remain faithful to a particular course of action even after it has become suboptimal. An extreme example of this was provided by the naturalist William Beebe who described a circular mill of army ants 350 m in circumference which persisted for 2 days and resulted in the death of many group members before eventually being broken, allowing the ants to move on. The conformity engendered by imitation may be broken either directly by negative feedback, as is the case with some species of ants that deposit repellent pheromones to prevent further recruitment to a trail (Robinson et al. 2005) or through random perturbations in the system. Randomness is recognised as an important component in self-organisation, since this can generate diversity across groups or yield novel opportunities which may then be amplified by positive feedback (Anderson 2002; Bonabeau et al. 1997). If the individuals currently engaged in some course of action have even a weak tendency to diverge from the existing course, then the shackles of conformity can be broken. To use the example of ants that are effectively trapped in the use of a suboptimal route, if individuals leave this path with even a low probability, and if these ants construct an alternative trail, then this may reset the behaviour of the group, if it is amplified through positive feedback. Beyond this, random perturbations are thought to be important in generating order. The concept of ‘order through noise’ suggests that a system will tend to reach a stable state more rapidly in the presence of random fluctuations than in their absence (Nicolis and Prigogine 1977; Yates et al. 2009). These feedback mechanisms and the associated nonlinear dynamics are what differentiate complex systems, as exemplified by collective behaviour, from systems where interactions between cause and effect are more predictable and which are therefore more amenable to the reductionist approaches of classical science (Heylighen 2013).

The structure of the group arises from its internal components rather than through external forces acting to control or shape it. This does not imply, however, that organisms within groups do not interact with their environment nor that feedback does not occur between individual-level interactions with the environment and the global structure of the group. Rather, it refers to the absence of deterministic, top-down control of the group. Indeed, group members must respond adaptively to environmental changes and to the existence of gradients within the environment if they are to maximise their own fitness. The ability to respond adaptively to such gradients, for example, to locate food or to thermoregulate by moving along a thermal gradient, is known to be enhanced by social interactions or, in some cases, exclusively a property of groups, since individuals are incapable of responding adaptively to certain gradients (Berdahl et al. 2013; Grunbaum 1998). In addition, there may often be interrelationships between the group and its environment, where the group modifies the environment, affecting the way that individuals respond to their environment and so shaping group-level patterns. The feedback cycle that results may extend in some cases to a form of niche construction (Odling-Smee et al. 2003). For example, many animals, including ungulates and humans, tend to form paths through their environment, which in turn influence the route taken by successive individuals through the environment, in many cases increasing the efficiency of the routes taken (Helbing et al. 1997). A negative outcome of the concentration of large numbers of animals is resource depletion. Large concentrations of fish or krill may contribute to a localised depletion of oxygen and an increase in waste products, particularly ammonium, that is at its most extreme towards the centre of stationary groups and would likely create conditions where individuals at the centre of such a group would migrate along a chemical gradient away from the group's centre (McFarland and Okubo 1997).

Self-organisation is not the only means of structuring group-level patterns and outcomes, nor does it always provide the optimum solution to a problem (Seeley 2002). A number of alternatives to self-organisation were presented by Camazine et al. (2001) including the imposition of external control over the actions of group members, through top-down leadership, through the possession by group members of some form of blueprint where an outcome can be envisaged and worked towards or through a template that guides the activity of group members, such as the responsiveness of ants to carbon dioxide build-up, described by Cox and Blanchard (2000). Where self-organisation does occur within a system, it may do so not because it is inherently superior to these alternatives but because that system lacks an effective global communication system to permit leadership or because the individuals within the system lack the computational ability to institute a global plan (Seeley 2002). Nonetheless, self-organising systems possess the virtue of being both robust and adaptable, enabling them to be responsive to fluctuating conditions. Self-organisation has provided remarkable solutions to some of the most intractable problems faced by animals and has yielded phenomena such as the bivouacs and bridges of ants, termite mounds, consensus decisions and, ultimately, the phenomenon of swarm intelligence. Self-organisation is a key reason behind the startling success of animals that live in groups.

3.4.1 Examples of Self-Organisation

Animal groups express a variety of self-organised patterns. These patterns are endlessly mutable and often ephemeral, since the systems are dynamic and the input provided by the component individuals is ongoing. Nonetheless, there are some broad categories of patterns that emerge through self-organisation. A key question relating to this is whether in each case the patterns have any functional importance or whether they may simply be regarded as epiphenomena. We introduce a non-exhaustive series of examples of self-organisation and discuss their functional relevance, if any.

3.4.2 Insect Foraging Trails

Eusocial insects provide some of the most compelling examples of self-organisation at work, the foraging trails created by ants being a case in point (see Fig. 3.3). The basic process underlying the formation of a foraging trail begins with an ant leaving its nest and exploring the local area in search of food. If the ant locates food, it then

Fig. 3.3 A trail of leafcutter ants (Bandwagonman at English Wikipedia [GFDL (http://www.gnu.org/copyleft/fdl.html) or CC BY-SA 3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons)

transports this back to the nest and, in the process, leaves a pheromone trail behind. The pheromone trail attracts other ants to the food source, and as they migrate between the food source and the nest, the trail is reinforced with additional applications of pheromone (Wilson 1971; Hölldobler and Wilson 1990). Generally, observations suggest that the trail tends over time to the most efficient route between the nest and food. Beckers et al. (1992a, b) examined this process of self-organised optimisation using black ants (*Lasius niger*), giving the ants a choice of two different pathways between a food source and their nest that varied in their length. They found that ants were responsive to even relatively small differences between the path lengths and consistently chose the shorter of the two routes. The explanation for this is straightforward – pheromones accumulate on shorter trails both because proportionately more are deposited per unit time and because since the trail pheromones are volatile, they evaporate over time. In a choice of routes as presented by Beckers et al., the greater amount of time spent travelling the longer route means that the pheromone has more time to evaporate in comparison to the shorter route. Ants encountering two diverging trails are more likely to follow the shorter trail which has the greater concentration of pheromone, so this route is gradually reinforced until the shorter route is selected almost invariably. This has inspired computational algorithms, in particular the ant colony optimisation algorithm, which are devoted to finding the best path through a network (Dorigo et al. 1996; Dorigo and Stutzle 2004). Argentine ants (*Linepithema humile*) demonstrated an ability to solve a more complex extension of the dual path problem posed by Beckers et al. when they were presented with a maze featuring 32,768 different paths between a food source and the entrance to a nest (Reid et al. 2011; see Fig. 3.4). Only two of these possible paths represented the optimum in terms of travel distance and time, yet almost all the colonies tested were able to find an optimal solution to the maze within an hour and were responsive enough to adapt to alterations to the maze that meant an alternative solution had to be found. This responsiveness comes in part through feedback mechanisms, which may amplify or suppress the probability of choosing particular paths. Additionally, individual ants may also deviate from the chosen path, which opens up the possibility of those ants locating alternative routes. If one of these routes offers a better alternative, it may in turn be amplified by positive feedback.

3.4.3 Lane Formation in Ants

The trails formed by ants, and indeed by other animals, require organisation if they are to function effectively, particularly if they feature traffic moving in both directions along the trail. This organisation is manifest in the formation of lanes in social insects and in human pedestrians (Jander and Daumer 1974; Couzin and Franks 2003; Helbing and Molnar 1995; Helbing et al. 1997). The regulation of traffic into lanes is exemplified by the foraging trails of army ants (*Eciton burchellii*) which may accommodate more than 100,000 individuals, some moving out from the nest to collect food and others going against this flow, returning to the nest with captured

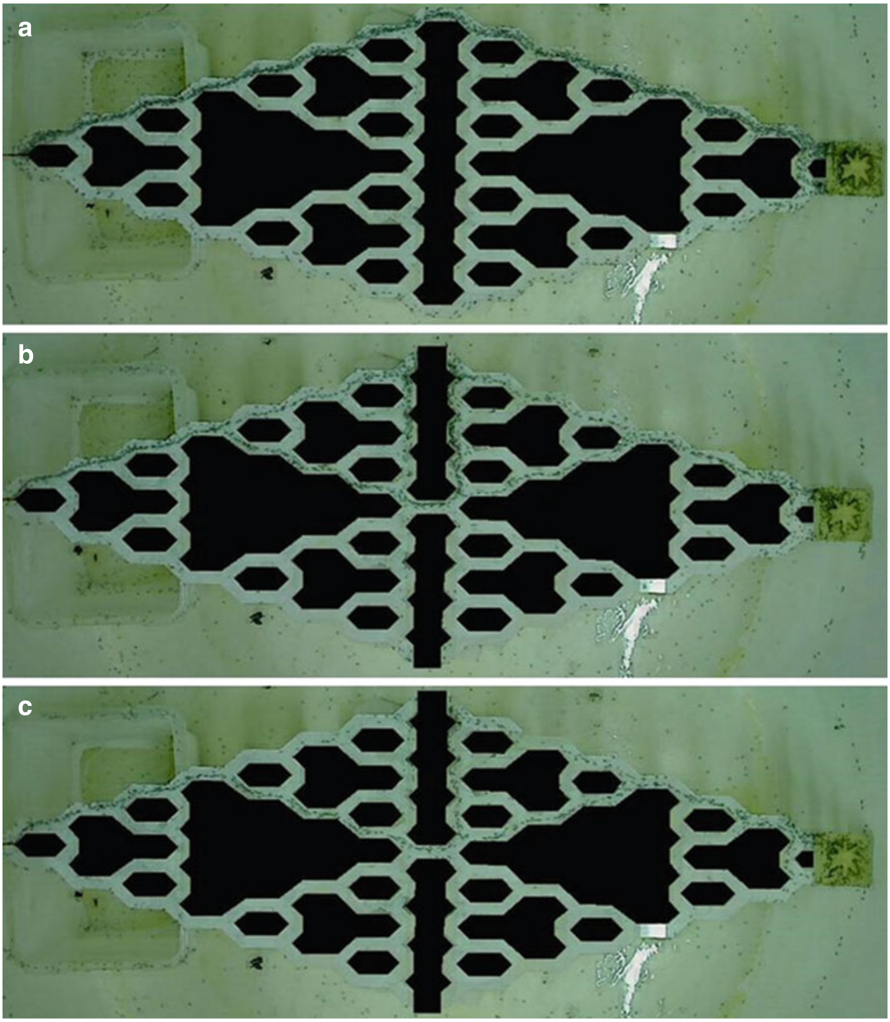

Fig. 3.4 Argentine ants are able to find the most efficient route even through complex mazes. In this example used by Reid and co-workers (2011), the ants move from their nest to the left of the picture through the maze to a food source on the right-hand side. In Box (**a**), the ants have selected a route along the top edge of the maze. In (**b**), however, this option has been removed and the ants have to adapt in order to solve the maze by moving through a newly installed central link in the maze. Subsequently, we can see in (**c**) that the ants are in the process of consolidating this new route (Photo copyright Chris Reid)

prey. Franks (1985) observed that returning ants move along the middle of the trail, while outbound ants move at either side of this central column.

The formation of army ant trails follows a similar pattern to that described previously for other ant species; it is mediated by the application and subsequent reinforcement of pheromones. Local interactions, in particular collision avoidance, structure the spatial arrangement of ants along the trail. As previously described, the ants are able to detect conspecifics at short range. When they detect another individual travelling in the opposite direction to themselves, they move aside. When a procession of two or more ants forms where each is entrained to walk in the same direction, transport is more efficient, since there are fewer stops and starts – as Helbing and Viscek (1999) put it, in respect of lane formation in humans: the system minimises the interaction intensity of the pedestrians. The establishment of lanes occurs through positive feedback, since the probability of an ant leaving one of these processions decreases as the size of that procession increases, so the processions grow and form into continuous lanes and the system can be said to have reached a more stable state. The development of the three-lane structure was explained in Couzin and Franks' (2003) model by reference to differences in the turning angles of outbound ants and returning ants when they encounter another ant, travelling in the opposite direction, which will likely be carrying prey. The outbound ants, which are not burdened with prey, exhibit a higher turning angle than the returning ants, and it is this simple heuristic which drives the migration of the outbound ants to the edges of the trail. The functional benefits associated with the basic process of lane formation are clear in terms of transport efficiency. Whether there is any further benefit to the formation of three lanes in army ants is open to discussion. One possible viewpoint is that the outgoing ants on the periphery of the trail effectively place a cordon between some kinds of opportunist scavenger and the food being conveyed back to the nest by returning ants. However, this does not serve to insulate the returning foragers from the attentions of various species of antbirds which kleptoparasitise the ants' catch (Wrege et al. 2005).

3.4.4 Group Morphology

The shape of groups arises through self-organisation, mediated by external influences from the physical environment, resource distributions and predator threat. There is almost endless variety in the shape of animal groups, yet there are consistent differences between taxa and some consistency within taxa. For example, many species of fishes, birds and midges form groups that move in three dimensions, yet the characteristics of their groups are very different despite the underlying assumption of broadly similar interaction rules between individuals across such groups. Differences are equally prevalent among species that move in two dimensions. Locusts in the grouping stage of their lives can form huge groups – marching bands of juvenile locusts can encompass billions of individuals (Uvarov 1977). The shape of these groups varies, but frontal structures, where the group form is characterised by a dense, narrow band that can be several kilometres in width, are common in both the Australian plague locust (*Chortoicetes terminifera*) and the desert locust (*Schistocerca gregaria*) (Buhl et al. 2011, 2012). Despite their huge size and numerosity, these bands are driven by simple local interactions over a relatively short range – each Australian plague locust aligns with individuals over a range of just 13.5 cm

(Buhl et al. 2011). Bazazi and co-workers (2008) demonstrated the importance of cannibalism as an organising principle in desert locust bands, since individuals who remain still may be attacked by other group members. This gave rise to an idea of collective motion in these species being driven by an escape and pursuit scenario, where each individual attempts to avoid being attacked from behind while simultaneously moving in pursuit of those in front. This contention was not supported by field data on Australian plague locusts (Buhl et al. 2012), possibly indicating species-specific differences in the way the animals interact.

Models of moving fish schools invoking attraction, repulsion and alignment between members predict an approximately oblong shape (Hemelrijk and Hildenbrandt 2012). This morphology is reasonably consistent across a range of different school speeds and compositions. The oblong shape is argued to emerge as a result primarily of local repulsion – fish leave a gap in front of themselves to avoid colliding with individuals ahead. In mobile, polarised groups, the effective repulsion zone in front of an animal needs to be greater than to either side, rather like cars travelling along a motorway. Across the entire group, this has the effect of elongating the shape into an oblong. This prediction is broadly supported by observations of fish shoals in the laboratory and in the wild (e.g. Partridge et al. 1980; Pitcher 1973a, b) including a study by Hemelrijk et al. (2010) on mullet (*Chelon labrosus*), examining the three-dimensional structure of schools of different sizes. At slower speeds, groups may generally become less ordered and less predictable. A model of herding behaviour in zebras predicted that groups moving at slow speeds would move in a phalanx, whereas as speed increases, a more regular group structure is predicted, which would have a similar profile to the fish groups described by Hemelrijk and Hildenbrandt (2012) (Gueron et al. 1996). By contrast, at greater speeds, Hemelrijk and Hildenbrandt predict schools should lose the oblong shape, becoming more teardrop shaped with a longer trailing tail. In addition, when groups are extremely large, group morphology also diverges from this oblong pattern.

In contrast to fish schools, and with the exception of the V-shaped formations of birds such as geese, bird flocks show very little consistency in space or time. The overall group morphology appears endlessly mutable, which incidentally may be why such flocks present such a mesmerising spectacle. Inspired by the dynamics of starling flocks, Hemelrijk and Hildenbrandt (2011) found that the shift in shape seen in airborne flocks can be explained by the dynamics of flight, and in particular, the turning behaviour of birds contributes to the variability in group shape. Unlike fish shoals, when bird flocks turn, the relative positions of birds in the flock are shifted and the overall shape of the group is changed (Pomeroy and Heppner 1992). In addition, as the flock increases in size, the flock may be effectively composed of subflocks that diverge from one another in their movements.

A fascinating study by Brierley and Cox (2010) found remarkable convergence in the morphology of aggregations of pelagic animals including both krill and fish. Over a thousand krill (*Euphausia superba*) swarms were examined using multi-beam sonar, enabling them to be characterised in three dimensions. These were compared to fish shoals examined using similar technology. The morphology of the groups was not a regular, geometric shape, but rather what the authors referred to as a ‘multifaceted lozenge’. Described in terms of roughness, or surface area to volume ratio, the similarity across a wide range of shoal sizes and densities was suggested to represent a potential universal response to factors experienced by all large groups in pelagic areas and in particular as a response to balance the need to migrate towards the centre of the group to minimise predation risk with the pressure to move in the opposite direction to avoid the oxygen-depleted core of large groups. Despite the similarity of such groups in terms of roughness, there may yet be sufficient consistent differences between species in terms of the morphology of the groups that they form to allow identification of species based on a snapshot of group morphology. (Guillard et al. 2011).

Another aspect of large groups is the emergence of self-organised structures involving a subset of the group’s members. An example of this is the wave-like patterns that form at the leading edge of migrating wildebeest herds. These patterns are generated by small perturbations which are then amplified into producing huge undulations across the front of the group. Despite the size of the pattern, the wildebeest interact with only a relatively few near neighbours – indeed, large interactions would tend to flatten the undulating front of these groups (Couzin and Krause 2003; Gueron and Levin 1993). Brierley and Cox (2010) reported more complex shapes emerging in groups of krill, such as a dumbbell shape and six- and eight-limbed spheres. Similarly, fish shoals seem to send out what Radakov (1973) referred to as ‘feelers’ where a proportion of the group initiates a new travelling direction and a process moves out from the group boundary. These initiatives may be abandoned, and those individuals return to the group, or they may be amplified through the group. Interestingly, when this amplification occurs, a common pattern is the formation of two dense groups, comprising animals that have moved and those that have yet to move, connected by a narrow neck of rapidly moving animals, so forming the dumbbell shape described by Brierley and Cox. Partridge (1981) raised the possibility that such patterns reflected the fact that large groups comprise several subgroups and that while individuals within subgroups may interact with others beyond that subgroup, such interactions are weaker than those that occur within subgroups. As yet, there is little direct evidence to support this contention but it remains a valid hypothesis.

3.5 Organisation and Structure of Animal Groups

Much of the internal structure of groups emerges through self-organisation. These include interrelated patterns such as the speed and alignment of group members and the density and the angle between them. Further measures include phenotypic and size assortment and the positioning of individuals in a group. Speed often plays an important role in this, since larger animals tend to move at a greater overall speed; this tends to lead to self-organised size assortment between groups and assortment with more similar individuals within groups (Krause et al. 2005). Hungry animals also tend to move more quickly than relatively satiated conspecifics, which can lead to the positioning of hungry animals at the front of groups (Hansen et al. 2015a, b; Krause et al. 1998a). We consider these aspects of group structure at greater length in Chap. 6.

3.5.1 Polarisation

In the context of animal grouping, polarisation is a measure of the alignment of group members. Indeed, the extent to which a group is polarised is sometimes taken as a proxy for its organisation. Pitcher (1983) used polarisation as a means to distinguish between shoals, being loose aggregations of fish, and the more ordered aggregations known as schools. In addition to polarisation, order in animal groups may be exemplified by the degree of collective rotation. In some cases, group members may rotate around their centre of mass, forming a structure known as a mill (or a torus in three dimensions). Mills have little polarisation at the group level, although they are aligned at local levels.

High polarisation in many groups emerges as group members increase their speed (Viscido et al. 2004), and indeed it is beginning to be recognised that speed regulation plays an important role in structuring collective motion generally. The strength of the response of animals to neighbours increases with speed, which, although not explicitly coded in most SPP models, may be an important factor in structuring group-level patterns (Herbert-Read et al. 2011; Katz et al. 2011). O’Brien (1989) reported that polarisation in swarms of crustaceans decreased in the presence of food and in the presence of a predator. In both cases, this may be the result of reductions in speed.

3.5.2 Density

Relative differences in density within groups may refer particularly to differences between the edge and the centre of a group or between the front and back of a travelling group. Numerous studies have reported greater density at the front of moving groups than at the back (Crofton 1958; Bumann et al. 1997; Hemelrijk and Hildenbrandt 2012). The picture is not quite so clear for patterns of density in the centre and at the edges of groups. Ballerini and co-workers (2008) reported that the edges of starling flocks were more dense than their interiors, which agrees with the observations of Soria and co-workers (2007) on bigeye scad (*Selar crumenophthalmus*) but is the opposite of the pattern observed by the same group of researchers on barred flagtail (*Kuhlia mugil*) where the density at the centre of the group is greater than at the edge, as predicted by most SPP models (Sumpter 2010). This lack of congruence between different species would seem to undermine suggestions of universality in patterns of grouping behaviour, despite the predictions of SPP models of broad similarities across species. The possibility remains that some of the patterns observed in laboratories do not necessarily reflect natural patterns of movement. The situation requires greater attention to be paid to the design of experiments in the field and the collection of high-resolution data on free-ranging animals.

3.5.3 Bearing Angle

The angle between an animal and its nearest neighbour in the group is often referred to as the bearing angle. Examining this across an entire group gives an idea of the spatial relationship of the group members. This has been measured for a wide range of different species (see Table 3.2).

It has been suggested that grouping animals with a strong social tendency are more likely to form highly structured groups featuring consistent bearing angles, compared to species with a weaker social tendency where the bearing angle would be far more variable (Dill et al. 1981). This contention lacks support at present but would certainly be worthy of additional study. Where animals do maintain consistent bearing angles between themselves and near neighbours and these angles repeat across the group, the animals may be seen to form into a kind of lattice.

Two main functions are proposed for this structuring pattern. Firstly, regular spacing in this manner may act to maximise the efficiency of information flow through the group by ensuring that the visual field is uncluttered. In such a structure, animals can perceive all near neighbours and can obtain salient information. Secondly, the structure may relate to aerodynamic, or hydrodynamic, efficiency. The calculated optimal bearing angles for locomotory efficiency have been achieved in the groups of some species (Cullen et al. 1965; Pavlov and Kasumyan 2000), but generally empirical data do not support the structuring of groups primarily to achieve this objective (Partridge et al. 1980; Usherwood et al. 2011). Nonetheless, studies have shown that despite the failure to conform to optimal predictions, travelling in a group can yield energy savings for individuals in trailing positions through drafting (Herskin and Steffensen 1998; Johansen et al. 2010). The bearing angle may therefore represent a trade-off between different needs: the ideal group structure for locomotory efficiency may not be the same as that for information transfer or the detection of threats (Abrahams and Colgan 1985). Further, the possibility exists that the bearing angle is an epiphenomenon emerging from the existence of the blind angle of the animals. Hemelrijk and Hildenbrandt (2012) suggest a

Table 3.2 Bearing angles measured between near neighbours in groups of different species

Species	Bearing angle	Reference
Sheep (*Ovis aries*)	55° ahead	Crofton (1958)
Starlings (*Sturnus vulgaris*)	90°	Ballerini et al. (2008)
Dunlin (*Calidris alpina*)	45°	Major and Dill (1978)
Cod (*Gadus morhua*)	90°	Partridge et al. (1980)
Herring (*Clupea harengus*)	45° and 135°	Partridge et al. (1980)

positive relationship between the size of the blind angle and the bearing angle. It would be informative to test this contention in grouping animals with 360° vision, such as soldier crabs (*Mictyris longicarpus*).

3.5.4 Transitions and Multistability

Analogies are often made between the structural organisation of animals in a group and the pattern of molecules in matter. For example, Gregoire et al. (2003) produced a self-propelled particle model and examined the properties of the group as a function of attraction strength. Where attraction was low, the particle moved freely like molecules in a gas; an increase in attraction caused the particles to coalesce into a liquid-like state and a further increase produced a fixed, lattice-like structure akin to molecules in a crystal. The analogy can be further extended to consider phase transitions – changes in the state of a physical system. For physical matter the conditions under which phase transitions occur are well understood, but can we predict the circumstances under which animal collectives undergo phase transitions?

We can consider two, non-mutually exclusive types of phase transition: first, the transition from disorder to order, where order describes a state of polarised and synchronised behaviour among group members, and, second, transitions between different group states. We described earlier the tendency of particles in Vicsek et al.'s (1995) and Couzin et al.'s (2002) models to make transitions according to changes in particle density and model parameters, but are the predictions of these models borne out by empirical data? Buhl et al. (2006) examined the movement of desert locusts (*Schistocerca gregaria*) in an annular arena and found that the collective patterns exhibited changed as a function of the density of insects in the arena. At low densities, the locusts showed little coordination with each other, but as density increased, order began to emerge, as predicted by Vicsek et al.'s model. At medium densities, the insects exhibited collective motion with periodic, self-organised switches in direction. As density increased still further, the tendency to switch direction disappeared, and the locusts became entrained to move in a particular direction. A simple mechanism for this density effect is that as density increases, the frequency of interactions (or collisions) increases, which favours the transfer of information and the adoption of more efficient (i.e. aligned) trajectories (Mann et al. 2013). Work on tilapia (*Oreochromis niloticus*) and herring (*Clupea harengus*) by Becco et al. (2006) and Makris et al. (2009) respectively also supports the notion of the emergence of order with increasing density; however, the results of a combined empirical and modelling study by Gautrais et al. (2012) on barred flagtails (*Kuhlia mugil*) predict reductions in social interactions at increased densities and an associated reduction in global order, suggesting that while disorder may transition to order according to density, the ordered state of the system may not be entirely stable in all cases.

Three main states are predicted by models featuring attraction, repulsion and alignment: swarms, mills and polarised groups. A swarm describes a pattern where group members are moving but the overall group remains in roughly the same place and is characterised by cohesion but little polarisation between members. Mills and toruses feature collective coordination of activity among members as individuals move around in a circle around an empty core. The third state is that of a group where members move collectively in a given direction and global polarisation is high. The model proposed by Couzin and co-workers (2002) demonstrated that transitions between these states could be effected by adjusting the size of the alignment zone while keeping the repulsion and attraction zones constant. As the size of the alignment zone increased, the particles would switch from a stationary swarm to a milling pattern and then eventually to a highly polarised moving group. The model demonstrated how comparatively small changes in the rules of interaction between individuals could result in dramatic shifts at the group level. Interestingly, this model also predicted the phenomenon of multistability, which describes how an identical set of local interaction rules can produce different patterns at the global level. In this case, the milling and polarised states could emerge from the same interaction rules. The predictions of the model were tested by Tunstrom et al. (2013) using golden shiners, in groups of 30–300 fish in a laboratory setting. At different times and as predicted, the shiners formed swarms, mills and polarised groups. The transition from swarming behaviour to either of the other two patterns was governed by an increase in swimming speed. However, this increase in speed and order coincided with a decrease in density, which is the opposite of the relationship described by Vicsek and co-workers (1995) and by Buhl and co-workers (2006). Moreover, the relationship between density and speed, negative in the study by Tunstrom and co-workers, was the opposite of that documented by Partridge et al. (1980), who found that the interindividual distance in schools of pollock decreased as the speed of the group increased. One difference between the studies that might explain these perplexing contradictions is that while the former examined a wide range of grouping states, the latter examined only the patterns existing in one state, that of polarised moving groups. Ultimately, the model prediction of multistability (or in this case, bistability) was supported by Tunstrom et al.'s experimental data; transitions between the different states were triggered by either the movements of a number of group members or interactions with the environment.

3.5.5 Synchronisation

A final example of self-organised behaviour is that of synchronisation, where animals coordinate their activities in time. Synchronisation is perhaps most apparent where an animal's activity can be reduced to a binary state, for example, moving/not moving or signalling/not signalling. Two animals may synchronise their activity so that they are in phase (i.e. both signalling at the same time) or out of phase (i.e. each signals when the other does not). There are many examples of such synchronisation in collective behaviour, including among human audiences, who synchronise their clapping behaviour (Neda et al. 2000). The mechanism for this was described by Kuramoto's coupled oscillator model (Kuramoto 1984), which explained that while individuals may have different patterns of periodicity in their expression of a behaviour, many can become entrained if each somehow adjusts their own pattern according to social feedback. Fireflies advertise for mates by producing bioluminescent flashes and they coordinate their flashes with near neighbours (Buck and Buck 1976). Similarly, cicadas (*Henicopsaltria eydouxii*) synchronise their calls with near neighbours such that waves of singing can be detected moving across the landscape (Herbert-Read et al. in prep).

Cole (1991) examined the activity patterns of ants (*Temnothorax allardycei*), finding that individuals seemed to show no consistent pattern of activity and that pairs placed together exhibited no sign of synchronisation, despite the fact that it is known that ants stimulate each other into activity. Nonetheless, in larger groups and at the colony level, the ants coordinated their activity to produce rhythmic patterns of activity with a periodicity of 26 min. A study on a related species found that there were different patterns of periodicity across the nest, with brood-care workers producing synchronised patterns of activity but those at the nest entrance much less so, since their activity was disrupted by the frequent arrivals and departures of foragers (Boi et al. 1999). These patterns of activity may help to evenly distribute brood-care effort (Hatcher et al. 1992) or to increase the efficiency of information transfer by allowing a greater number of ants to interact (Franks and Bryant 1987). Synchronicity in the behaviour of animals plays an important role in shaping the dynamics of grouping behaviour and is in turn shaped by the local environment and by the internal state of the animals themselves (Conradt and Roper 2000). In a study on chacma baboons (*Papio ursinus*), King and Cowlishaw (2009) provide a fascinating insight into the relationship between individual activity and group-level behaviour. They found greater likelihood of synchronous behaviour across groups early in the day, when the animals were intent on foraging, and that the animals were more synchronised in woodland as opposed to open habitat, which may relate to the foraging strategies of the animals in woodland (King et al. 2009), and when the groups were more cohesive.

3.6 Summary

Our understanding of collective behaviour has undergone a transformation in recent times, and recent technological innovations mean that empirical approaches to test the predictions of models, until recently impossible, are now within our grasp. In this regard, the opportunity exists to determine how the existence of differences between individuals in terms of their physiology, their temperament and their internal state, including aspects such as nutritional state, affect the expression of behaviour, particularly in a social context. Information gathered using sensor tags can integrate real-time physiology and movement data, allowing us to examine how these aspects shape the way in which individuals interact with other group members, and how they scale to affect group-level processes. While laboratory work will continue to provide valuable insight, opportunities now exist to study animal collectives in their natural environments, in turn bringing greater biological realism to our understanding of collective behaviour.

At the heart of research into collective animal behaviour is the need to relate the behaviour of one level of biological organisation – the individual – to the behaviour of the other level, the group. The interacting individuals cause patterns to emerge at the group level. As these emergent patterns typically have no single, unique set of causes, making them complex and often unpredictable, this presents a problem that we need to consider in a different way to many others in the study of animal behaviour. Nonetheless, insights are possible as we gain greater understanding of the organising principles that structure the interactions of the individual elements in the system and use this information to identify elements in group behaviour that are consistent across events.

Social Foraging and Predator-Prey Interactions

4

4.1 Introduction

The social environment has a substantial effect upon the ability of animals to find and hold on to food and other vital resources. At the same time, grouping can play an important role in determining how likely individuals are to end up becoming prey for others. Many animals are both predator and prey and must face the challenges of foraging and responding to the threat of predation simultaneously (Beauchamp 2013). The first part of this chapter considers matters from the perspective of the forager. When animals forage together, their success, both in terms of finding resources and actually getting to consume them, is likely to be affected by the presence and behaviour of their group mates. Here we use the term forager in a very broad sense. While a good number of the examples we cite consider predators – animals that actively search for and consume other living animals – most of the concepts we discuss are relevant to scavengers, herbivores, detritivores and drift feeders too. Indeed, most of the principles discussed in this chapter may also be applied to animals that are searching for mates, water, minerals, nesting materials, tools or any other contestable item or resource that they may require in order to function. In some cases, different lines of research have emerged to deal with different types of resource, each with their own terminology. For example, the ways in which foragers interact and shape one another's behaviour have been widely studied within the framework of social foraging (Giraldeau and Caraco 2000), while courtship and competition for mates have been considered under the umbrella of communication networks (McGregor 2005). We suggest that many of the costs and benefits of foraging together that we discus in the following sections will apply widely to many or all of these different resources, although of course the finer details of how competition for these actually plays out will depend upon the behaviours being studied and the species concerned. In the second part of this chapter, we focus upon the antipredatory costs and benefits to prey animals of grouping. At the very end of the chapter, we consider mixed-species groups, the evolution of which appears to have been driven by a combination of social foraging benefits and the need to avoid predators.

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4.2 From the Perspective of the Forager

One of the key advantages to foraging in groups is access to information, for example, about resource distribution, quantity and quality. This can benefit individuals if it improves the efficiency with which they search. For those that produce such information, this can also be a cost, if it permits others a chance to scrounge or steal the resources that they have found. Foraging in groups can also be advantageous if it allows predators to overcome prey defences or to work together to catch large or dangerous prey that individuals alone may not be able to tackle. Competition for finite resources is often the key cost of social foraging. This can take a number of forms, from simple depletion of a common resource to kleptoparasitism and direct aggression. It can have indirect effects too: individuals may be compelled to accept more risk when foraging as competition intensifies, or else they may search with lower efficiency, as they monitor and avoid others who may steal from them or attack them. In some cases, owing to their spatial positioning relative to others, individuals may find themselves in the shadow of competitors who are able to access resources before them. Finally, large groups of foragers may be more readily detected by their prey, and the passage of multiple predators may trigger prey to seek refuge, rendering them unavailable to other hunters in the group.

4.2.1 Access to information

Alongside antipredator benefits, discussed later on in this chapter, perhaps the greatest advantage to foraging in a group is access to information. Information is a vital currency for foragers; the means to effectively locate resources and discriminate between those of lower and higher quality are likely to be favoured by selection if they translate into increased foraging efficiency. As they forage, animals produce cues that can alert others as to the location of resources. In some cases, successful foragers may actively signal that resources have been found. This may occur if it benefits foragers to recruit others to join them at a resource patch. The conditions under which recruitment may occur are discussed in Chap. 7. It is likely however that in the majority of cases, these cues are produced passively. That is, they are produced inadvertently as a by-product of the forager's behaviour as it interacts with the environment and exploits the resources that it has found. Observers that detect these cues and join the forager can be thought of as information parasites or scroungers. Where animals are able to identify group mates that have found food, so long as they are able to obtain a share of it, it may benefit them to forage in large groups. This is because larger groups are expected to find food faster, since the greater the number of searchers, and the greater the area or volume of space that they occupy, the faster they will encounter resources (Pitcher et al. 1982; Cvikel et al. 2015). Moreover, animals in larger groups may search more efficiently, more intensively or more widely, whether due to facilitation through reduced predator vigilance costs or because they are compelled to do to compensate for higher levels of competition (Grand and Dill 1999; Webster and Laland 2012; Herbert-Read et al. 2013).

There are very good reasons as to why animals should make use of social information generated by others. Searching the environment directly can be costly both in terms of time investment and exposure to predation risk and other hazards. It may therefore pay individuals to join others that have found resources or to exploit the same types of resources that they exploit if they are able to do so. On the other hand, indiscriminately copying others is not an adaptive strategy in the longer term (Giraldeau et al. 2002). This is because the distribution and quality of resources can change between locations and over time, meaning that socially transmitted information may quickly become outdated. Foraging decisions based upon obsolete information may be suboptimal or even maladaptive. In the laboratory, naïve guppies (*Poecilia reticulata*) follow and learn the routes travelled by their shoal mates and persist in using these even after shorter routes are made available (Laland and Williams 1998). Young and inexperienced bobolinks (*Dolichonyx oryzivorus*) use the calls of experienced older males when selecting breeding territories and can be experimentally induced to settle in and defend suboptimal territories using audio playbacks (Nocera et al. 2006). Finally, basing foraging decisions solely upon socially transmitted information may lead foragers to overlook resource patches that may be more productive than the ones that they have seen others exploiting. The evolution, mechanisms and function of social information use and social learning, and the conditions under which selection is expected to favour social information use, continue to receive a great deal of attention from researchers. Detailed reviews of this field are provided by Valone and Templeton (2002), Danchin et al. (2004), Laland (2004), Hoppitt and Laland (2008, 2013) and Rendell et al. (2011). Here we focus upon several key concepts in social information transmission: local enhancement, public information use and the information centre hypothesis.

4.2.1.1 Local Enhancement

Local enhancement is generally defined as the attraction of an animal to locations where it can detect or has previously detected other individuals (Hoppitt and Laland 2008). Precise definitions vary (see also, e.g. Thorpe (1956) and Galef (1988)), but we suggest that the one presented here captures the way that the term is most commonly used in the behavioural ecology literature today. Many social animals show a tendency to approach others irrespective of whether they are foraging or not, and in many cases local enhancement may be a by-product of such social attraction. Local enhancement need not therefore occur solely for foraging reasons. Nevertheless, for many species, it is probably an important component of social foraging behaviour. Even over short distances and especially over longer ones, feeding animals may be more obvious than the resources that they are exploiting and for which the forager is searching. It may therefore pay foragers to move towards groups of conspecifics, since under some conditions, these may be a reliable proxy for the location of resources. As such, local enhancement can operate across a range of levels, from tens of kilometres to the very fine scale, within the area occupied by the foraging group itself.

At the landscape scale, local enhancement when searching for food may be especially important for some birds, such as pelagic seabirds (Thiebault et al. 2014) or carrion feeding vultures (Houston 1974; Jackson et al. 2008). This is because aerial aggregations may be more readily detectable than the food over which they are gathered. In other species of birds, those in flight may use the presence of conspecifics that have alighted upon the ground to locate food patches. Furthermore, some species may be able to use the posture or behaviour of conspecifics in order to determine whether or not they are feeding, information that can affect their decision to join them or not. This has been demonstrated in great blue herons (*Ardea herodias*); although they are normally solitary predators, individuals will join others that are feeding (Krebs 1974). Visual cues may be less readily available over long distances to terrestrial animals, whose field of vision may be disrupted by the topography of the land, or to aquatic animals, since attenuation of light in aquatic environments can severely limit visibility. Here, local enhancement may operate through other sensory modalities, such as hearing or detection of chemical gradients.

Local enhancement is an important process at finer scales too. Dispersed groups of foragers can search for resources both directly and indirectly, by monitoring the behaviour of nearby group mates, exploiting the cues that they produce as they feed. In spice finches (*Lonchura punctulata*), birds that have found food move their heads up and down as they handle and consume it, a reliable cue as to the location of food that can be exploited by others (Coolen et al. 2001). The relationship between searching for resources directly and looking out for others that have found them is captured by the producer-scrounger family of models, in which the producers search for food and the scroungers monitor their discoveries, using this information to move in and steal from the producers. Individuals can act both as producers or scroungers, and in some cases they may switch between the two modes of foraging or do both simultaneously (Vickery et al. 1991), while in others they may tend to specialise as one or the other (e.g. Giraldeau and Lefebvre 1986). The relative proportion of producers and scroungers operating within a group at any given time exists in a state of dynamic equilibrium, since the fitness return of one role depends upon the frequency of the other. When producers are most common, it may pay to scrounge since there will be lots of opportunities to do so. When most members of the group are scroungers, however, competition between them is likely to be high, because there are many of them and the amount of food being discovered by the few producers is low. Under such conditions, it may be better to be a producer, especially if the producer is able to consume some of the food, the so-called finder's share, before the scroungers arrive to compete for it (Barnard and Sibly 1981; Vickery et al. 1991; Di Bitetti and Janson 2001). Laboratory experiments have shown that flocks of birds can converge over time on the predicted stable equilibrium ratio of producers to scroungers for a given food distribution. Mottley and Giraldeau (2000) allowed three captive flocks of spice finches to socially forage for seeds. The feeding rate of scrounging birds was highly

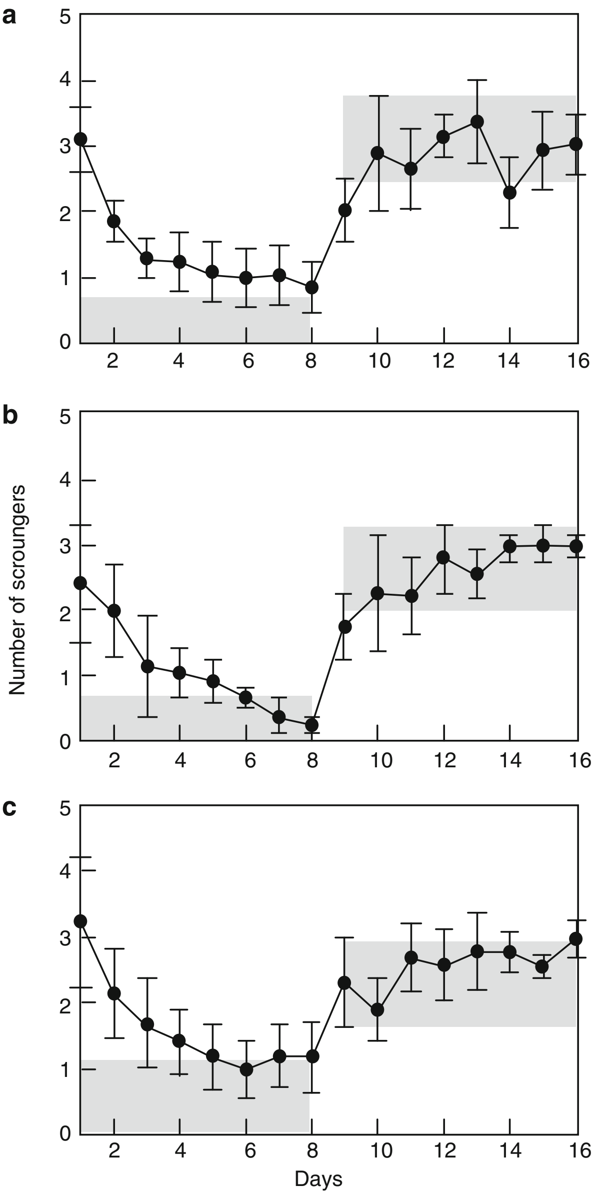


Fig. 4.1 The number of spice finches using scrounging tactics (mean +/– SE). Data are shown for each of the three flocks (**a**–**c**), containing six individuals each. The finches were tested in an apparatus that allowed them to alternate between producing and scrounging behaviour. On days 1–8, the scroungers access to the patches was limited, while on days 9–16, the patches were more readily accessible to the scroungers. Lower rates of scrounging were therefore favoured on days 1–8 than on days 9–16. The *shaded areas* show the predicted stable equilibrium frequencies for scroungers. The birds converged on these after a few days' experience of the foraging apparatus (From Mottley and Giraldeau (2000))

negatively frequency dependent with respect the number of birds that were using scrounging tactics at any given time, while the feeding rate of producers showed little or no decline with scrounger frequency. Birds alternated between producing and scrounging and within a week or so the groups converged upon the stable equilibrium frequency of the two tactics (Fig. 4.1).

4.2.1.2 Local Inhibition

While local enhancement deals with the tendency of animals to move towards locations where others are or have been, the opposite effect can occur too, with animals actively avoiding locations where they have detected others. This has been termed local avoidance or local inhibition. Local inhibition may be an important means by which foragers avoid searching for resources in locations that have recently been visited by others and which may have already been exploited. In some stingless bees (*Meliponini spp.*), for example, foragers avoid visiting flowers that have recently been exploited by colony mates and which may be temporarily depleted (Slaa et al. 2003; Biesmeijer and Slaa 2004). Local inhibition can also be an important process in shaping how social foragers avoid conspecifics that may kleptoparasitise or behave aggressively towards them and may also be an important process in mitigating against prey depression in some species. The effects of competitor and aggressor avoidance upon foraging efficiency are discussed in a little more detail below.

4.2.1.3 Public Information About Resource Quality

Foragers may use socially transmitted information not only to locate resources but also to assess their quality or quantity, relative to other options. The ability to use social information to assess quality may benefit individuals in a number of ways, not least by allowing them to make comparisons without the need for potentially costly direct sampling (Valone and Templeton 2002). Animals may use social information for relative quality assessment in the short term, for example, when moving between prey patches, as well as in longer-term decisions, such as where to locate breeding territories. Indeed, in the case of the latter, social information use has been suggested to be a significant driving force behind the formation of breeding colonies (Danchin and Wagner 1997), with breeders establishing nests in areas where breeders in previous years have successfully raised many or high-quality young (Doligez et al. 2002; Aparicio et al. 2007; Calabuig et al. 2008). Returning to foraging, in the shorter term, foragers may use social information to select between prey patches that differ in their productivity. This has been extensively studied in ninespine stickleback fish (*Pungitius pungitius*). Sticklebacks that were allowed to watch two groups of conspecifics foraging at patches that yielded prey at different rates were shown to be able to discriminate between the richer and poorer patch using conspecific feeding behaviour alone, tending to approach and remain in the richer patch. This was the case both when the feeding conspecifics were still present and also after they and the food had been removed, indicating that the sticklebacks had learned the location of the rich patch (Coolen et al. 2003; Laland et al. 2011).

4.2.1.4 Groups as Information Centres

Animals that forage independently but which share communal roosts, nests or shelters may inadvertently transmit information about resources that they have found to their roost mates when they return. Under such conditions, the communal shelter can be thought of as an information centre (Ward 1965; Ward and Zahavi 1973). While it was originally through that individuals may be able to recognise successful foragers and follow them when they next set out to forage, some researchers have argued that the evidence for this effect is overstated (Richner and Heeb 1995). Nevertheless, convincing support for an information centre function for group living is provided by a few studies. One concerns the colonial breeding cliff swallow (*Hirundo pyrrhonota*). Here, unsuccessful foragers were seen to return to the colony and subsequently follow more successful colony mates in order to locate prey. The followers may identify successful foragers by the numbers of insects that they bring back to the colony to feed to their chicks (Brown 1986).

Beyond following others, there may be other mechanisms by which information is passed between animals sharing shelters about the availability, quality or palatability of resources in the environment. A huge body of work by Galef and colleagues (Galef and Wigmore 1983; reviewed by Galef 1996, 2009) has shown that brown rats (*Rattus norvegicus*) tested in the laboratory are able to socially acquire food preferences through smelling a particular food type on the breath of a conspecific that has recently eaten it (Fig. 4.2). Rats acquire preferences for novel foods that they have not encountered before if exposed to them in this way. The implication of this work is that the shared resting places of rats may act as information centres wherein conspecifics can learn about which foods in their environment are good to eat. It would be informative to test these predictions in wild or commensal populations of rats, now that the technology exists to do this. In a similar experiment, this time focussing upon another rodent, the dwarf hamster (*Phodopus campbelli*), one member each from a number of a breeding pairs was trained to forage for two types of food, each of which was placed in its own unique location. Only one of the two foods was available on each day. The partner of the forager was then allowed to eat and store the food that was available on that particular day – this served as a cue to the forager as to which food was present, and they subsequently were more likely to approach and search in the location of that particular food (Lupfer-Johnson et al. 2009). Evidence for social enhancement of food preferences has been found in other species too, including domestic dogs (*Canis familiaris*, Lupfer-Johnson and Ross 2007) and in short-tailed fruit bats (*Carollia perspicillata*, Ratcliffe and ter Hofstede 2005), suggesting that the social assemblages of these animals may also potentially have an information centre function.

4.2.1.5 Other Benefits of Foraging in Groups

Foraging in a group may allow group members to collectively overwhelm the defences of resource holders. Solitary juvenile ravens (*Corvus corax*) can be excluded from a food resource, such as a carcass, by territorial pairs of adults. The response of juveniles to this is to recruit others so that they are able to gain control of the carcass by weight of numbers (Heinrich and Marzluff 1995). In a similar way, territorial dusky damselfish (*Stegastes dorsopunicans*) defend algal mats, preventing potential competitors from foraging in the area. While solitary fish have little chance of overcoming the attentions of the territory holder, groups of blue tangs (*Acanthurus coeruleus*) are able to do so if they invade the territory en masse. The feeding rate of the tangs in these instances is positively correlated with group size, as in larger groups; each individual tang receives relatively fewer attacks (Foster 1985).

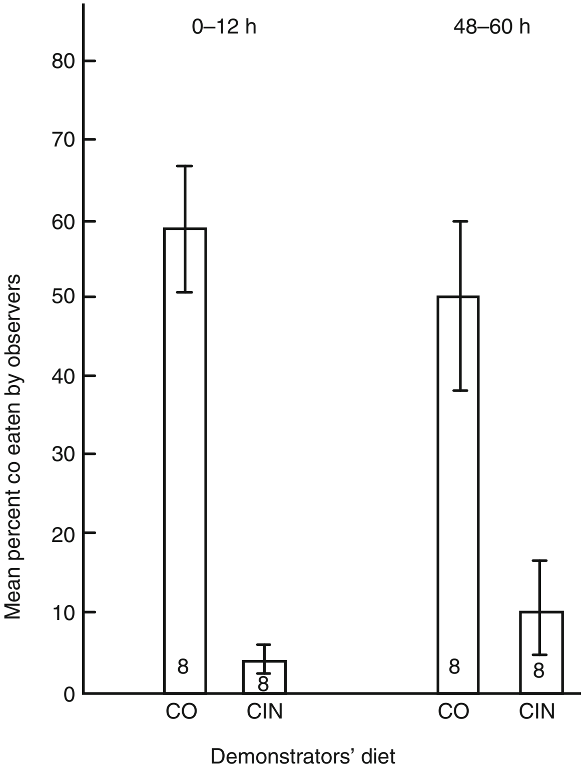


Fig. 4.2 The percentage (mean +/− SE) of the total food eaten that was flavoured with cocoa by test subject rats in trials in which they were given the choice of eating cocoa (*CO*) or cinnamon (*CIN*)-flavoured food. The test subjects had never eaten cocoa or cinnamon-flavoured food previously. Prior to being tested, they were exposed to demonstrator conspecifics that had been fed with food containing one of these two flavours. When the test subjects were given the opportunity to feed, they ate more of the food type that had been eaten by their 'demonstrator' rat. More than half of the food eaten by test subjects exposed to cocoa-fed demonstrators was also cocoa-flavoured up to 12 h after exposure. Rats exposed to cinnamon-fed demonstrators predominantly ate cinnamon-flavoured food themselves, an effect that was also apparent at up to both 12 and 60 h after exposure (From Galef and Wigmore (1983))

Predators that hunt in groups can in some cases exploit larger or more difficult-to-catch prey than they otherwise could if they hunted alone. They may achieve this through coordinated behaviour, or it may be an outcome of the independent actions of many predators. Groups of predators may be more likely than lone animals to succeed in subduing prey of a given size and may even be able to capture larger prey that would be impossible for individuals to tackle. Analysis of records of more than 800 hunts by six packs of African wild dogs (*Lycaon pictus*) revealed that the size of prey captured was positively correlated with the number of adults in the hunt, while the mean chase distance decreased as the number of hunters rose (Creel and Creel 1995, Fig. 4.3). In addition to this, larger groups of predators might also be

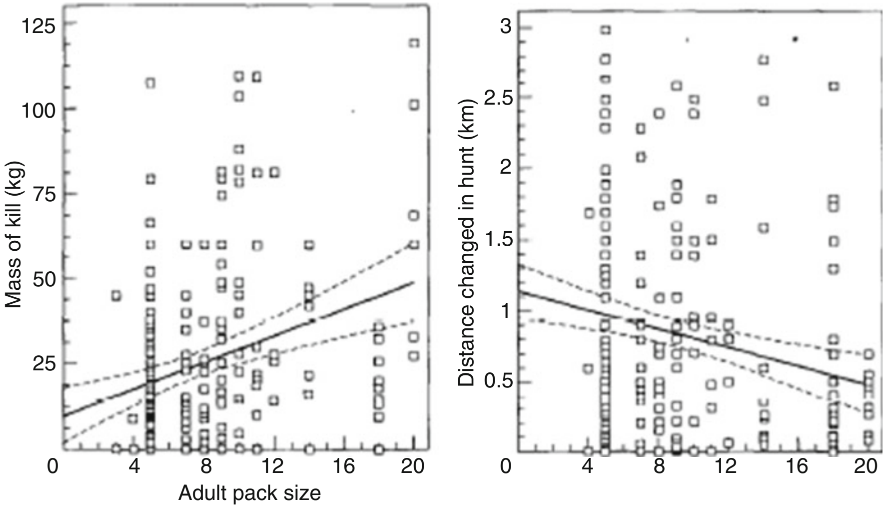


Fig. 4.3 The mean mass of prey killed by packs of wild dogs increased with increasing pack size (**a**), while the distance the prey were chased for before being captured decreased (**b**) (From Creel and Creel (1995))

better able to defend their prey against con- and heterospecific competitors. For example, larger groups of lions (*Panthera leo*) are better able to defend carcasses from groups of spotted hyenas (*Crocuta crocuta*, Cooper 1991). In some cases this advantage may be outweighed by other factors, in groups of African wild dogs, the benefit of being able to defend kills from hyenas in terms of food available per individual was offset by the increase in competition among pack members (Carbone et al. 1997).

Animals that hunt in groups can capture and handle prey not only through sheer numbers but also by effectively coordinating their behaviour in order to circumvent prey defences. This type of cooperative behaviour is reasonably widespread and is even theorised to have driven the evolution of sociality in some species (Packer and Ruttan 1988). In one ecotype of orca (*Orcinus orca*), individuals coordinate their movement, creating waves that flush seals and penguins from ice floes into the water where they can be captured (Visser et al. 2008). Chimpanzees (*Pan troglodytes*) hunt smaller primates in a coordinated fashion with some individuals acting as drivers, flushing prey towards other group members who wait in ambush (Boesch 1994). Within lion prides some females have been seen to adopt stalking roles, outflanking prey before initiating chases and driving them towards waiting females who tackle the prey in flight as it comes within range (Stander 1992). Spotted sea trout (*Cynoscion nebulosus*) attack schools of menhaden (*Brevoortia patronus*) in processions. Attacks cause the groups of menhaden to fragment, reducing their capacity to perform collective antipredator behaviours and reducing confusion and related effects that otherwise limit predator hunting success (Handegard et al. 2012). Groups of predators do not necessarily need to coordinate their behaviour in order to overcome prey defences. Duffy (1983) describes diving behaviour of a number of species of seabirds upon schools of pelagic fish that plausibly might have the dual effects of fragmenting the schools into smaller units from which the predators are better able to track and capture individual fish and also of fatiguing the fish, as they respond to repeated dives, making them easier to catch.

4.2.2 Competition for Resources

If antipredator benefits (discussed later in this chapter) and access to information are the two primary benefits to group living, for many species the greatest cost is competition. This can take a number of forms, and these may operate simultaneously. Groups of animals may simply use up resources faster, while individuals may also steal from one another or aggressively contest ownership. Competition can have more subtle effects too. Competing individuals may attract further competitors or predators or pay the costs of divided attention, being less likely to notice their approach. They may have to modify their behaviour if they are to avoid rivals, at the cost of reducing their foraging efficiency. Finally, the presence of many foragers may drive their prey to seek cover more frequently or for longer, placing them beyond reach. These costs are explored in more detail in the following sections.

4.2.2.1 Depletion

The amount of a resource that is available to a forager is dependent upon the number of others that are also exploiting it, and larger groups should be expected to deplete resource patches sooner than small ones. Where resources are depletable, scramble competition may occur with group members foraging rapidly so as to consume as much of the resource as possible before it is used up. The relationship between forager number and resource depletion rate may not always be perfectly linear. In some cases, social facilitation and reduced per capita investment in vigilance for predators may result in greater individual resource intake rates as a group size increases, such that larger groups deplete prey patches at disproportionately greater rates than smaller ones. Counteracting this, kleptoparasitism, aggressive competition and the indirect effects of individuals seeking to avoid such interactions, discussed below, may serve to reduce average individual foraging efficiency, such that above a certain group size or density, the patch depletion rate may begin to slow. Predicting the rate of patch depletion then requires knowledge of the number or density of individuals within the group, the yield of the patch and the nature of the interactions that take place between the group members at different group sizes. It should also be noted that not all resources may be depletable or else may only be depleted by unusually large groups of foragers or groups that remain in a fixed location for an unusually long period of time. It is interesting to consider that some prey species may even have evolved to take advantage of this, by synchronising breeding, emergence or migration in order to swamp predators and maximise the likelihood of them or some of their relatives or young surviving (see the Sect. 4.3.2).

Where resources are finite, the costs of depletion may not be borne equally by all of the foragers within the group. Different group members will likely differ in their abilities to effectively compete for resources, resulting in skewed foraging success between individuals. Superior competitors may therefore be able to gain enough of a given resource even when it is scarce or when there are many others in the group and may therefore be less susceptible to the costs of depletion compared to their group mates. In groups of rainbow trout (*Oncorhynchus mykiss*), individuals that consumed a greater share of food on average also showed less variability in food intake in comparison to poorer competitors, and this effect was stronger when less food was available (McCarthy et al. 1992).

A consequence of competition for depletable resources may be a shift in the speed-accuracy trade-off faced by foragers as they select between high- and low-quality food items. Selecting prey that turns out to be inedible or which yields very little energy may be costly, and when prey is plentiful, it may pay animals to be more discerning, investing time in inspecting prey or food before deciding whether to handle it. When competition is more intense, however, the costs of foregoing edible food may exceed the costs of being wrong, and foragers may accept a greater rate of false positives. The investment of time or energy associated with investigating and then rejecting food may be low in the short term, but may accrue over the longer term. For some species, there may be other follow-on costs too, such as exposure to predators; a fish that rises from the reef to inspect every passing object may capture more prey on average than a shoal mate that breaks cover to feed less frequently, but it may also run a greater risk of being captured by a passing predator. To our knowledge, this has not been explicitly tested. Drift-feeding riverine fishes, which must regularly distinguish between edible and inedible items as they pass by and which regularly inspect and reject drifting items (Neuswanger et al. 2014), could represent a useful model system for addressing such questions.

4.2.2.2 Interception/Shadow Competition

Interception competition typically occurs between animals that are somewhat restricted in their movements, and which forage by waiting for prey to approach them, intercepting it as it passes by. Those individuals that are positioned such that they encounter the prey first have the opportunity to capture it, rendering it unavailable for those behind them. This effect has been described in drift-feeding salmonid fishes, where dominant individuals occupy upstream sites (e.g. Hughes 1992; Elliott 2002). It is sometimes also known as shadow competition, since those individuals that are downstream in the current lie in the shadow of those individuals that are upstream of them and which can access for drifting prey first. In principle, interception competition may occur in other systems too. In groups of competitors, those on the periphery of the group may be better positioned to intercept prey (or other resources such potential mates) before those on the group interior. This effect can be seen as the flip side to Hamilton's (1971) selfish herd concept, where peripheral individuals pay the cost of being the first to encounter predators, too. Interception competition may also affect terrestrial ambush predators. In the burrowing spider (*Seothyra henscheli*), those on the interior of burrow clusters grow more slowly, most likely due to the effects of those occupying outer burrows encountering and consuming prey first (Lubin et al. 2001). Interestingly, aggregated ambush predators may also stand to benefit from the proximity of conspecifics under certain conditions; Rao (2009) describes a ricochet effect among orb web spiders (*Argiope keyserlingi*) in which prey sometimes rebounds off an outer web and lands on an inner one. By building their webs close enough to rivals, these spiders may be able to offset much of the cost of interception competition.

4.2.2.3 Kleptoparasitism

Kleptoparasitism refers to the stealing of a resource from one individual by another. This may be a food item, nesting material or any other transportable item over which animals may compete. While kleptoparasitism is generally considered a cost of social foraging, from the perspective of the kleptoparasite, the opportunity to steal resources while forgoing the costs of searching for and handling them can obviously be advantageous. For the victim of the kleptoparasite, there can be a number of costs. First of all, there is the loss of the contested item. Where rates of kleptoparasitism are severe, this can lead to animals selecting smaller or more easily handled prey, which, although they contain less energy, can be consumed before others have a chance to steal it, as has been described for foraging kelp gulls (*Larus dominicanus*, Steele and Hockey 1995).

Even if the kleptoparasite is not successful in stealing the item, it may be destroyed, be lost, escape (in the case of living prey) or be stolen by a third party. This can be disadvantageous to both the kleptoparasite and the target of the kleptoparasite, with the targets bearing more of the cost, as they will usually have invested more time in searching for and handling the object. It has been suggested that the compounds released from the damaged skin of some ostariophysan fishes that have been injured by predators may have a disruptive function, encouraging kleptoparasitism by attracting further predators that might compete with the first, affording the prey an opportunity to escape (Mathis et al. 1995).

The costs of kleptoparasitism may not always be immediate, but may become apparent later on, depending upon the function of the contested resource. Colonially breeding chinstrap penguins (*Pygoscelis antarctica*) build nests using stones. Males steal stones from rival nests and add them to their own, while also attempting to defend them from others. Small nests are more vulnerable to flooding which can occur following snowmelts, which in turn can lead to the failure of eggs to hatch or the death of chicks and the loss of the parent's reproductive output for that season (Moreno et al. 1995).

The nature and distribution of the contested items are likely to influence the prevalence of kleptoparasitism among groups. When contested items are abundant, easy to find and easy to process, then we might expect kleptoparasitism to occur less frequently. Among shoals of three-spined sticklebacks, rates of kleptoparasitism were higher when food items were made available sequentially than they were when the same number of prey items was made available simultaneously. Over a 4-week period, levels of kleptoparasitism dropped in the sequential food treatment, but remained constant in the simultaneous food treatment. This suggests that familiarity between group members, which might facilitate the development of dominance hierarchies, also plays a role in mediating food stealing behaviour in this species, albeit only under certain food distributions (Webster and Hart 2006a).

When prey items are costly to handle, then it should pay kleptoparasites to be sensitive with respect to the timing of any attempted theft. It is to their advantage to allow the victim to pay the costs of handling the object and to only attempt a theft once the object has been processed. A kleptoparasite that intervenes and steals an object too early, such as a nut with a tough shell, must then pay the time and energy costs of processing it and may itself become the victim of another kleptoparasite while doing so. This idea is formalised by Broom and Ruxton's (2003) 'apple and orange' model. When a forager has found a food item that must be processed before it can be consumed (represented by the orange, which first must be peeled before it can be eaten), then kleptoparasitic attacks should be focussed towards the end of the handling period. If a forager has a food item that it can begin to consume immediately (the apple, which can be eaten without the need for peeling), then kleptoparasites should attempt to steal it as soon as possible, before the edible parts are depleted. The model predicts that when food is common and easy to find and when aggressive contests are longer, kleptoparasitism will occur less frequently and that it will increase with forager density when animals are exploiting 'apple'-type foods and decrease when they are feeding on 'orange'-type foods.

4.2.2.4 Aggressive Prey Contests

Another major cost of competition, for one or both parties, can be aggression. Aggressive competition over resources can be costly in a number of ways. Most obviously, fights between large or well-armed species may end to death or debilitating injury. Lethal or injurious aggression may also occur when the fitness payoffs of winning are especially great to both participants, such that it may pay to escalate and persist in competing. This may apply when food is very scarce, for example. This idea has specifically been tested among broods of chicks in species known to practise obligate or facultative siblicide. Findings have been mixed; in brown boobies (*Sula leucogaster*), dominant chicks were more aggressive and more likely to expel their siblings when they received less food (Osorno and Drummond 2003); however, this pattern is not seen in great egrets (*Casmerodius albus*) or great blue herons (*Ardea herodias*) where aggression was unrelated to food provisioning levels (Mock et al. 1987).

Aggression can also have other, indirect costs. It can heighten predation risk, both because aggressive behaviour can be conspicuous to predators and also because individuals that are engaged and aggressive competition might be less vigilant and therefore less likely to detect approaching predators. Both the cichlid fish, *Nannacara anomala*, and the willow warbler (*Phylloscopus trochilus*) were less likely to detect approaching model predators when involved in aggressive

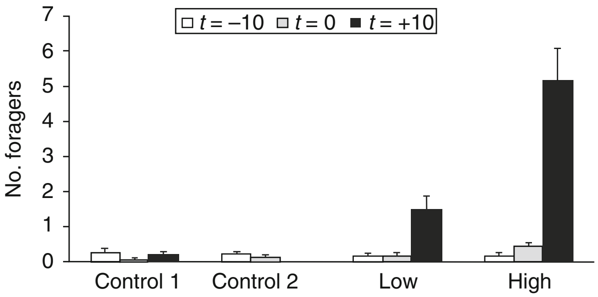


Fig. 4.4 The number of hermit crabs present within experimental plots 10 min before (*white bars*) immediately before (*grey bars*) and 10 min after (*black bars*) simulated commotion. Commotion was simulated by jostling empty shells held on strings in a way that simulates the movement of occupied shells as the crabs within them compete for resources. Control 1 was an empty patch with no shells present, while in Control 2 shells were present but were not moved. In the low and high commotion, conditions were simulated by jostling the shells 4 or 20 times per 10 s. These data suggest that hermit crabs may be attracted to areas where conspecifics are competing over resources (From Laidre (2013))

interactions, behaviour which under natural conditions, may translate into increased risk of mortality (Jakobsson et al. 1995; Brick 1998). In the terrestrial hermit crab *Coenobita compressus*, simulated aggressive competition between individuals competing for food and shells acted as an attractive stimulus not to predators but to other conspecifics, who gathered in areas where simulated levels of competition were highest, an effect that might be expected to intensify local competition (Laidre 2013, see Fig. 4.4). Finally, the need to engage in or avoid aggression may impart significant opportunity costs to individuals. Less dominant individuals may need to spend time hiding from would-be aggressors or may be forced to search for resources in suboptimal areas. Such indirect effects of aggression and of competition in general are discussed below.

4.2.2.5 Prey Depression

Prey depression occurs when, having detected predators, prey animals seek refuge and cannot be detected or captured by them until they re-emerge; hence, the availability of prey is reduced or depressed. As the number of predators at a patch increases, the frequency with which prey animals detect predators should also increase, causing them to spend more time in refuge. This effect has been studied in redshanks (*Tringa totanus*), wading birds that forage on coastal mudflats, where they feed on amphipods (*Corophium volutator*) that live on or close to the surface of the sediment. The amphipods can seek refuge by moving deeper into the mud, where they are out of reach of them redshanks' probing beaks. The prey capture rate of redshanks in areas that have recently been searched by other birds initially drops, before gradually increasing again as a function of time elapsed since that area was last visited (Selman and Goss-Custard 1988). The initial drop and slow return of prey capture rates reflects the effects of gradual recovery from prey depression. A

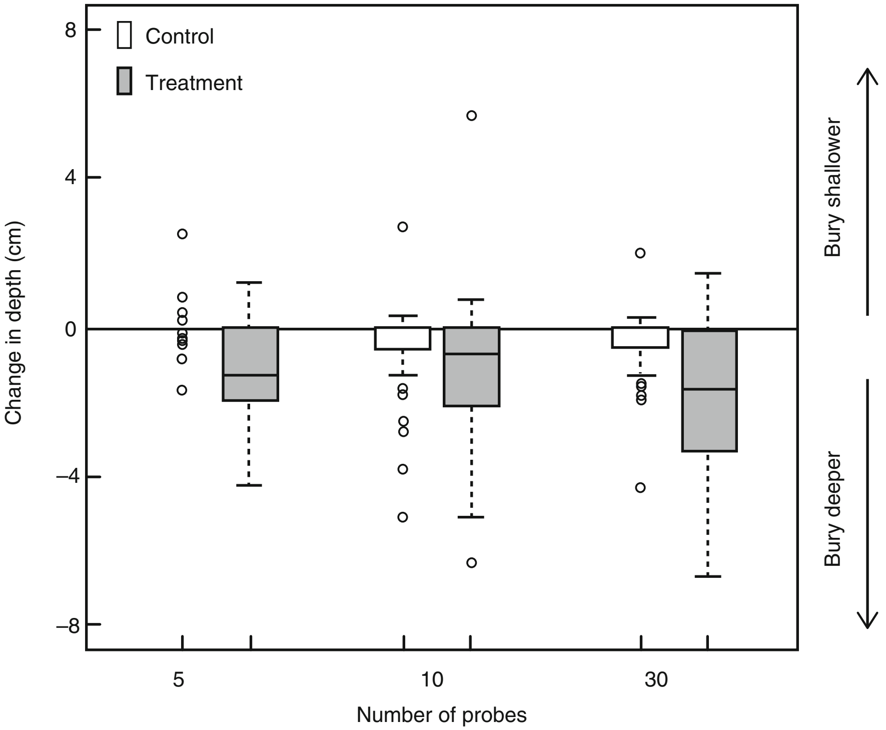


Fig. 4.5 The change in depth (median, quartiles, 10th and 90th percentiles, outliers) of lugworms in response to manual probing of the substrate (simulating the probing bills of wading birds) in a laboratory experiment. Probes were made into experimental aquaria, while neighbouring control aquaria were not probed. As probing rate increased, median depth increased too (From Duijns and Piersma (2014))

similar response was seen in lugworms (*Arenicola marina*), in response to predation pressure from another wading bird, the bar-tailed godwit (*Limosa lapponica*) – in the field, experimental probing resulted in lugworms producing fewer casts, suggesting that they were spending less time in near the surface. This was confirmed through laboratory experiments, where the lugworms were seen to produce deeper burrows in response to experimental probing (Duijns and Piersma 2014, see Fig. 4.5). Predators may be able to overcome the effects of prey depression by following search paths that avoid areas that they themselves or others have recently visited (Stillman et al. 2000). The need to track the movements of others may come at the cost of reduced prey detection if predators cannot scan for prey and conspecifics simultaneously, though if this is less costly than the effects of prey depression, then predators may be expected to do so.

4.2.2.6 Other Indirect Effects of Competition on Foraging Efficiency

Animals may suffer reduced foraging efficiency resulting indirectly from their attempts to avoid foraging in areas that have been or are likely to soon become

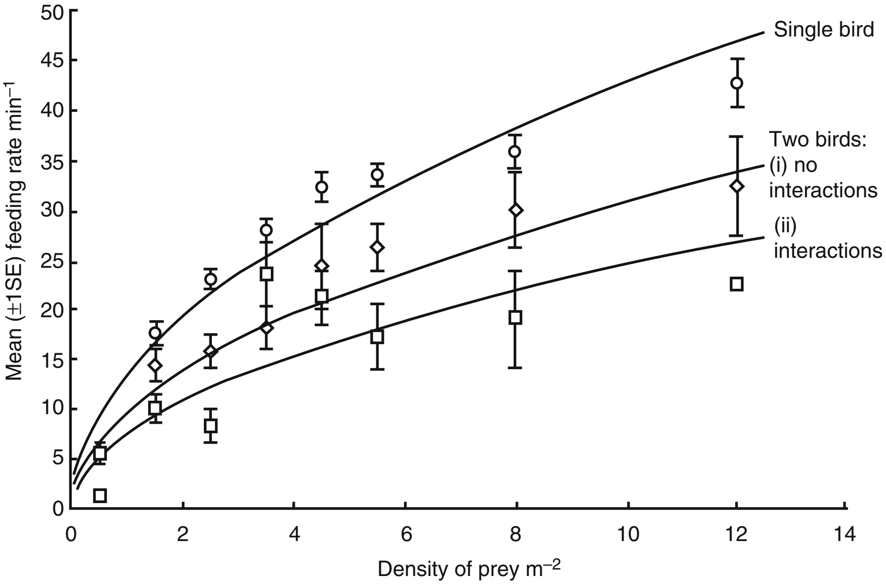


Fig. 4.6 The mean (+/− SE) feed rate across a range of prey densities of blackbirds feeding alone, with another non-interacting bird nearby or with an interacting competitor present (From Cresswell (1997))

depleted. They may instead focus upon foraging in lower-quality patches, which contain fewer other foragers, but where resources are also less abundant or of lower quality. Under such conditions, we might expect that selection should favour mechanisms by which individuals are able to optimise their foraging rate while accounting for both the quality of different patches and the distribution of other foragers between them. This idea is captured by the ideal free distribution concept (Fretwell 1972; Parker and Sutherland 1986).

In addition to avoiding depleted areas, foragers may also modify their behaviour so as to avoid encountering others that might attack them or steal their food. This may occur if they avoid areas containing other foragers, which may in turn lead them to forage in less profitable areas, as discussed above. Alternatively, they may forage close to others, offsetting the risk of being attacked or kleptoparasitised by tracking the locations of their group mates so as to take evasive action if necessary. If searching for food and maintaining vigilance for kleptoparasites or aggressors are mutually exclusive activities, foragers must alternate between them, reducing their overall foraging rate. This has been demonstrated for European blackbirds (*Turdus merula*), where individual food intake was substantially lower when a competitor was present at the same patch, even in the absence of direct, aggressive interactions (Cresswell 1997, 1998, Fig. 4.6). Such effects may be exacerbated by the need to frequently change direction so as to avoid others and may cause foragers to search with greater redundancy than they otherwise might, passing through areas that they have already visited and depleted.

Finally, foragers may render resources unusable to their group mates in ways other than by consuming them, for example, by contaminating them with faeces or urine as they pass over them. Other foragers may avoid these if they are unpalatable or toxic or if they contain parasites. Sheep (*Ovis aries*) avoid grass that has been contaminated with conspecific droppings and focus instead on clean patches (Hutchings et al. 2001). As a consequence, much of an otherwise usable resource is underexploited.

4.3 From the Perspective of the Prey

Alongside foraging benefits, protection from predators can be a major advantage of living in groups. Indeed for many species, protection from predators may be the key or the only benefit gained from grouping. Here we consider how prey group size might affect the likelihood of being detected by a predator, the risk to individuals of being attacked, and how these two effects can be accounted for together, using the concept of attack abatement. We then go on to consider other ways in which grouping can facilitate detection, confusion and repulsion of predators. In broad terms, selection might be expected to favour behaviours and other adaptations that serve to minimise the likelihood of detection by predators, of being attacked if detection does occur and finally of being captured, if attacked. The ideas discussed here are also pertinent to group-living predators of course.

4.3.1 Encounter Dilution, Attack Dilution and Attack Abatement

4.3.1.1 Encounter Dilution

Can prey animals reduce the risk of being detected by predator by forming groups? This putative benefit of grouping is known as encounter dilution (Pitcher and Parrish 1993) or predator avoidance (Krause and Ruxton 2002). If we assume that grouped and single prey animals are equally difficult to detect, an assumption that may not often be realised (see below), then the rate at which an actively searching predator encounters members of a fixed-sized population of prey should be expected to decrease if they are clumped together compared to if they are more evenly dispersed through space. It is not clear, however, whether this should translate into a lower likelihood of being detected for grouped prey individuals. If larger groups are indeed equally as likely to be detected as smaller groups or lone individuals, then while the presence of groups in the population should reduce encounter rates with predators overall, this should be expected to affect all prey irrespective of the size of a group that they are in. Once detected, prey that are in larger groups may gain other benefits, such as a diluted risk of being targeted, discussed below, but these are separate from their initial likelihood of being detected by the predator.

The effect of prey group sizes upon encounter rates with predators was studied in a laboratory experiment by Ioannou et al. (2011). They found that stickleback predators orientated towards and approached larger groups of (dead) chironomid larvae at greater distances than they did for smaller groups, suggesting that they are better able to detect larger groups than smaller ones. However, they also found that this risk to larger groups of being detected was more than offset by the fact they were on average further away from searching predators in treatments where the finite prey population was divided into larger but fewer groups. This study provides a useful framework for making predictions about grouping and encounter dilution that can be applied to other predator-prey systems. It is probably often the case that larger groups are more likely, or at the very least not less likely, to be detected by predators at a given distance than smaller ones. This may be because larger groups of animals simply present a greater stimulus, by occupying a greater volume of space, making them easier to see, or because they produce more noise or chemical or other cues that the predators can detect. They may also behave in quantitatively or qualitatively different ways than smaller ones, such as by engaging more frequently or intensively in competition, aggression or courtship behaviours that may make them more conspicuous to predators. Perhaps somewhat mitigating against this effect is the fact that as the number of groups falls, as animals form into larger but fewer aggregations, the distance between a group and a predator will be greater on average at any particular moment, as Ioannou et al. (2011) report. This effect may be influenced by environmental heterogeneity, however, which may constrain prey dispersal or provide predators with information about their likelihood of encountering prey in any particular area, guiding their search strategies and increasing their encounter rates.

There are other ways in which grouping may dilute encounter rates with predators. If predator search strategies incorporate a time limit which leads them to quit a patch and search in a new area if prey are not detected within a given period, then clustering, if it leads predators to go longer in between detecting groups, may benefit prey by causing predators to give up and forage elsewhere (Taylor 1984). Krause and Ruxton (2002) suggest that low encounter rates caused by prey clustering may also lead predators to switch to alternative and more readily discoverable prey types.

4.3.1.2 Attack Dilution

Although grouped prey may be found less often than the same number of solitary prey, the total risk experienced by an individual will depend on how many individuals a predator can kill each time a group is found. In general, the likelihood of any one individual being targeted or captured is expected to be lower in larger groups. Though this may broadly hold, in nature the relationship between group size and per capita risk is unlikely to be perfectly inversely proportional to the size of the group. First, this effect can only apply in cases where the predator is incapable of capturing all of the individuals in the group at once. A flock of birds that discovers an aggregation of caterpillars, for example, might rapidly consume all of them in one feeding bout – under such conditions, attack dilution effects will probably not be present. This idea is discussed further with reference to area-limited search tactics by predators later on in this chapter. Second, all individuals are not equally likely to be targeted by a predator. Predators may preferentially target weak, young or injured individuals. They may be more likely to attack those that are on the periphery of the group or which are further from their nearest neighbours. This possibility forms the basis of the selfish herd theory (Hamilton 1971) discussed in more detail in Chap. 6. They may also target individuals who look or behave differently from the rest of the group; this is known as the oddity effect. Predators may also prefer to target individuals who appear to be less vigilant (Krause and Godin 1996). Finally, attack dilution effects will only apply if the rate at which groups receive attacks is not closely positively correlated with the number of individuals that they contain. If, for example, a group of ten animals is attacked by predators ten times more often than a lone animal, then individuals would do just as well not to form groups, all else being equal. If the frequency of attacks is disproportionately positively related to group size, then grouping would actually become disadvantageous and it could pay for prey animals to actively avoid one another.

4.3.1.3 Attack Abatement: Accounting for Encounter Dilution and Attack Dilution Together

A number of authors have argued that the benefits that individuals gain from grouping in terms of encounter dilution and attack dilution can only be fully understood when the two effects are considered together, taking into account both the likelihood of a group of a particular size being detected in the first place and, following detection, the per capita risk of a group member actually being captured (Turner and Pitcher 1986; Wrona and Dixon 1991). This combined effect is known as attack abatement. This is illustrated in Fig. 4.7, which considers a population comprised of two groups of animals, one containing only a single individual and the other containing four individuals. It assumes that the likelihood of being targeted and captured is inversely proportional to the number of individuals in the group, such that the lone individual is always captured if it is detected, while in the group of four, each individual has a one in four chance of being the one that is eaten. In terms of being initially detected by a predator, however, a number of different scenarios are examined. In cases where the single individual and the group of four are equally likely to be detected by a predator, then it pays individuals to group so as to benefit from attack dilution effects. If the likelihood of a group being detected is linearly proportional to the number of individuals that it contains, then individuals can expect to do equally well by remaining alone or by joining a group. What if the groups are disproportionately more likely to be detected by predators? If groups are far more likely to be detected by predators, then the benefits in terms of attack dilution that are gained by grouping may be offset by the much higher likelihood of being attacked. Under such conditions, it may pay individuals not to join groups at all. If on the other hand groups are disproportionately more likely to be detected by predators than are individuals, but the increase in the rate of detection relative to increasing group size is low enough, then it may still pay individuals to form groups; even though they are attacked more often, the likelihood of any one individual being killed is still lower than it is for lone animals. In many systems, this latter scenario is likely to be the most common. For example, Wrona and Dixon (1991) reported such an effect in interactions between sedge fly (*Rhyacophila vao*) pupae and their

Scenario		One prey 	Group of four prey 	Does it pay to group?
Prey group size does not affect likelihood of detection	Risk of encountering predator (e)	0.5	0.5	Yes
	Risk of being captured (c)	1	0.25	
	Total risk (e x c)	0.5	0.125	
Likelihood of being detected is linearly proportional to group size	e	0.2	0.8	An individual could do equally well by grouping or remaining alone
	c	1	0.25	
	e x c	0.2	0.2	
Likelihood of detection increases disproportionately with group size: e.g. every additional individual doubles the likelihood of detection	e	0.11	0.89	No-remain alone
	c	1	0.25	
	e x c	0.11	0.22	
Likelihood of detection increases with increasing group size, but at a rate lower than 1:1 e.g. a group of 4 is twice as likely to be detected than a single individual	e	0.33	0.67	Yes
	c	1	0.25	
	e x c	0.33	0.16	

Fig. 4.7 Attack abatement: the benefits of grouping in terms of protection from predators depend both upon the risk of being detected and the risk of being captured following detection. Both are affected by group size. Here, different scenarios are presented which consider these factors together. In some cases, it pays to group with others, while in other cases doing so may be costly, and it may be better to avoid others and remain alone

planarian predator *Polycelis coronata* – larger groups were attacked more frequently, but attack dilution effects within such groups meant that risk of predation was nevertheless lower compared to that faced by pupae in smaller groups.

4.3.2 Predator Swamping

When predators have to handle prey before they are able to consume them, this places a limit on the maximum number that can be caught within a given period of time. Here handling refers to any of stalking, pursuing, subduing, killing and digesting prey. Even if handling costs are minimal, there is likely to be an upper limit on the number of prey that a predator needs to or is capable of eating within a particular period of time. Prey may take advantage of this by synchronising their behaviour with respect to exposing themselves to predation risk. Doing so may mean that large numbers of individual prey animals are present during windows of vulnerability, diluting the risk for any one individual of being captured. This is known as predator swamping, since far more prey are available than the predators are capable of capturing. If, instead of emerging together, prey animals were to stagger their emergence over a much longer time period it is expected that overall prey mortality would be higher.

Evidence for such effects is variable, and predator swamping may drive the evolution of synchronised behaviour in some systems, but not in others. On the one hand, metamorphosing western toads (*Bufo boreas*) tended to emerge sooner and in clusters when predatory garter snakes (*Thamnophis sirtalis*) were present, suggesting a potential swamping function (Devito et al. 1998). Snowshoe hares (*Lepus americanus*) have high reproductive synchronicity, and juveniles born closest to the mean population timing of birth had lower mortality than those born later on (O'Donoghue and Boutin 1995). Great horned owls (*Bubo virginianus*) take a similar biomass of common tern (*Sterna hirundo*) chicks across the breeding season, even though the number of chicks available is around one hundred times greater at its peak than at the start. When chick numbers are low, this can translate in up to 100 % mortality through predation by the owls, suggesting that synchronised breeding offers a swamping effect against the steady background rate of predation (Nisbet 1975). On the other hand, Tucker et al. (2008) found no difference in survival of hatchling red-eared terrapins (*Trachemys scripta*) that were released en masse compared to those that were allowed to emerge naturally in a more sequential fashion. In a second experiment, they found that terrapins released in staggered groups actually had higher survival compared to those released en masse. With specific reference to breeding synchronicity, Ims (1990) argues that overall mortality from generalist predators might actually increase with breeding synchronicity, especially if within colony synchronicity is greater than that between nearby colonies, suggesting that some other factor drives breeding synchronicity in such species.

Mass emergences can lead to superabundance of prey, and predators may potentially take advantage of this, for example, by switching to solely focus upon these prey types, by travelling to locations where mass emergences occur, by consuming far more prey than they normally would, by storing uneaten prey to consume later or by synchronising their breeding seasons to coincide with prey emergence. The mass emergence of periodic cicadas (*Magicicada* sp.) is a spectacular natural phenomenon that is thought to serve a predator swamping function (Williams et al. 1993; Williams and Simon 1995). Some authors have suggest that the emergence periods of these cicadas, being prime numbers of 13 and 17 years, have evolved because this minimises the likelihood of predators synchronising their own breeding cycles with those of the cicadas (e.g. Goles et al. 2001). More recently, however, other researchers have argued that prime-number periodicity in these species most probably evolved to minimise the risk of hybridisation between different species (Yoshimura et al. 2009).

4.3.3 Detecting Predators: The Many-Eyes Effect

Larger groups may be more effective at detecting approaching predators compared to smaller ones (Lazarus 1979; Treherne and Foster 1981). They may be better able to more accurately identify hidden predators at a greater distance or more likely to spot them sooner as they approach. Several studies provide evidence for this latter effect; where groups are smaller, predators (or the predator-like stimuli used by experimenters) are able to close to a shorter distance before individual group members began to change their behaviour, for example, by adopting alert postures or fleeing. Larger flocks of laughing doves (*Streptopelia senegalensis*) detected an approaching model raptor sooner than smaller ones (Siegfried and Underhill 1975), while larger groups of emus (*Dromaius novaehollandiae*) detected approaching humans (experimenters standing in for predators) sooner than small groups (Boland 2003). In detecting predators while they are still fairly distant, prey animals may be able to undertake appropriate actions, such as fleeing, mounting defences or signalling to the predator that it has been detected. The latter action may occur in systems where predators rely upon surprise to capture prey and where moving away to another area is costly to the prey. Under such circumstances, it may be beneficial to both predator and prey to avoid the energetic costs of, respectively, an unsuccessful pursuit and unnecessary evasive action. Thomson's gazelles (*Eudorcas thomsonii*) that have detected stalking cheetahs (*Acinonyx jubatus*) often approach and follow them. Followed cheetahs tend to move away from the area of the inspecting gazelles, rather than continuing the stalk and launching a chase (Fitzgibbon 1994). Glowlight tetras (*Hemigrammus erythrozonus*) produce conspicuous 'fin flicks' upon detecting chemical cues from injured conspecifics, and predators are less likely to attack these presumably more alert individuals (Brown et al. 1999).

The enhanced ability of larger groups to detect approaching predators probably occurs both because at any given moment, there are likely to be more individuals scanning for danger than there are in smaller groups and because they may be able to pool their imperfect information in order to more accurately identify threats (Ward et al. 2011). This is known as the 'many-eyes effect'. Once an individual has detected a predator, it may transmit this information to others in the group, either passively, by adopting antipredator behaviour that others are able to detect and respond to, or in some cases actively through communication via an alarm signal or call. The apparently paradoxical outcome of the many-eyes effect is that it can simultaneously increase the level of vigilance at the level of the group, while reducing the amount of time spent by any one individual group member being vigilant. This is because the many-eyes effect (acting in concert with other antipredatory grouping effects) enables individuals that are in larger groups to reduce the amount of time that they spend looking out for predators without paying the cost of increased risk of being preyed upon (Roberts 1996). Note that the sensory modality by which prey animals detect predators need not of course be vision. In some cases auditory, chemical or tactile cues may be more important in predator detection, and many species are likely to integrate information from several different sensory systems at the same time when detecting and tracking threats. A related point is that it is not always clear to what extent scanning for predators and engaging in other behaviours such as foraging, courting or mating can be performed effectively at the same time. For prey species where vision is of primary importance, it may be the case that they cannot simultaneously search their immediate surroundings for food or competitors and watch the horizon or sky above them for predators or that, if they can, they do so with reduced effectiveness. For example, when brown trout (*Salmo trutta*) were housed with familiar group mates with whom they engaged in fewer aggressive interactions they responded sooner to incoming attacks from a model predator compared to comparison groups housed with unfamiliar fish (Griffiths et al. 2004). This suggests that their attention is divided between looking out for competitors and predators and that when the vigilance costs imposed by one of these are relaxed, they are better able to deal with the other. Creel et al. (2014) found that for some east African ungulates, including Grant's gazelle (*Nanger granti*), the proportion of foraging individuals at any given moment fell as vigilance increased. However, for prey animals which rely upon detecting chemical cues both to find food and identify predators, such a trade-off may not exist. Similarly, this may be the case for species that rely upon one sensory modality for detecting food at close range and other, different sensory modalities for detecting approaching predators over greater distances. There is scope for further research into determining the extent to which the many-eyes effect operates among groups of animals that primarily rely upon different or multiple sensory channels.

Group members can only benefit from the many-eyes effect if they are able to recognise when other group members have identified predators. They may do this by responding to cues produced by others who have detected danger. These may range from the cessation of feeding or other behaviours, the adoption of scanning postures, changes in orientation, production of alarm calls or fleeing. European minnows (*Phoxinus phoxinus*) respond to the skittering and inspection behaviour of conspecifics that have detected predators by reducing feeding behaviour and seeking refuge (Magurran and Higham 1988). Eastern chipmunks (*Tamias striatus*) exposed to playbacks of conspecific alarm calls, produced when predators have been detected, vacated the area and then assumed alert postures, with the strength of their response being affected by the duration of the alarm calls and the number of simulated callers (Weary and Kramer 1995). As individuals are able to respond to the antipredator behaviour of their group mates, it is not necessary that all individuals directly detect the predator for the whole group to be able to mount a response. Ocean skaters (*Halobates robustus*) are an aquatic insect that aggregates to form flotillas on the surface of the water. Their response to predators is to increase speed and turning rate, behaviours which may have a confusion effect function (see below). Skaters that have not detected the predator directly exhibit these behaviour too when they detect conspecifics doing so, such that the response rapidly propagates through the flotilla, at a rate greater than that of the approaching predator (Treherne and Foster 1981). The authors termed this behaviour the Trafalgar effect, after the use of signalling by Admiral Nelson's fleet to communicate information about enemy movements to ships that were too far away to directly observe them. Herbert-Read et al. (2015) studied the propagation of escape waves through shoals of Pacific blue-eyes (*Pseudomugil signifer*) as they swam through an annular arena. The ring layout ensured that when a fright stimulus was presented at one point, it was only visible to a small proportion of the shoal, which was dispersed along a larger sector. The initial reaction of the fish that saw the fright stimulus was to orientate away from it and accelerate. This response passed as a wave through the whole group, causing its members to turn away and speed up, even though most of them had not seen the stimulus directly, suggesting a simple mechanism based upon local interactions by which the whole group can mount an antipredator response.

Because of the value of such socially transmitted information in some systems, it may be the case that individual's vigilance is geared towards collecting information about the antipredator behaviour of a group mates as well as towards detecting the predators themselves.

Finally, predators may be able to offset their prey's many-eyes advantage by preferentially targeting prey that does not appear to be vigilant. Guppies (*Poecilia reticulata*) that were foraging from the substrate in a head-down posture detected an approaching model predator at a closer distance than did those that were not feeding and had their heads up. Furthermore, predatory acaras (*Aequidens pulcher*) preferred to attack head-down guppies over non-feeding head-up fish and were more successful at capturing these (Krause and Godin 1996a; Fig. 4.8). For this reason, it may pay all individuals to engage in some vigilance, even if they are members of a very large group. The targeting of prey animals when they are engaged in feeding and therefore being less vigilant may be one reason behind the evolution of the fascinating cooperative vigilance behaviour of rabbitfish (*Signanus* sp.). When these fish forage as a pair,

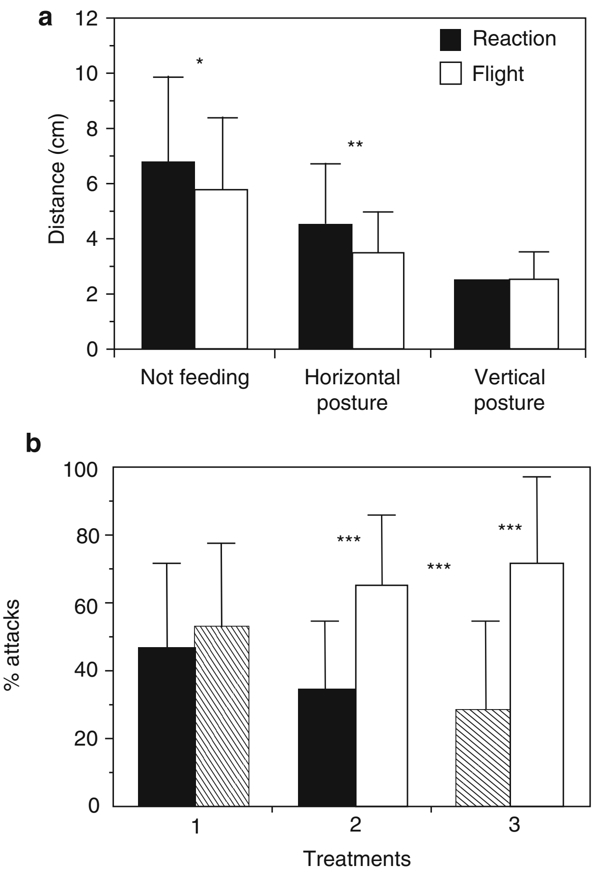


Fig. 4.8 (**a**) The distance (mean +/− SE) at which guppies reacted to and fled from an approaching model predator as a function of whether and how they were feeding. (**b**) Pair-wise comparisons of predatory acaras' preferences (mean +/− SE) for attacking non-feeding versus horizontal feeding, non-feeding versus heads-down feeding and horizontal versus head-down feeding guppies (*black, hatched and white bars* respectively). *, **, *** indicate $P<0.05$, 0.005, 0.001 (From Krause and Godin (1996a))

each individual takes turns either feeding or being vigilant. This allows the forager to take more bites at the algae or sponges on the substratum, increasing its foraging efficiency relative to solitary conspecifics (Brandl and Bellwood 2015).

4.3.4 The Confusion Effect and the Oddity Effect

The confusion effect describes the difficulty faced by the predator of processing information on prey location or movement such that it becomes less able to single out a target both as prey group size increases and (arguably of greater importance) as the appearance and behaviour of individual group members become more similar, resulting in a lower attack to success ratio. This effect may occur because of limitations upon predators' ability to gather information on and anticipate the movements of many individuals simultaneously. Confusion effects may be especially powerful where targets travel against a moving background formed by their group mates, where the movement path of a single target interweaves with the paths of other individuals which may be crossing it and travelling in different directions or where the target is frequently occluded by other individuals.

Neill and Cullen (1974) showed that for a number of fish and cephalopod predators attacking shoals of smaller prey fish, their attack times increased, while their encounter rates with prey fell as prey group size increased, suggesting that attacks are less effective when directed against bigger groups. In a comprehensive set of experiments focussing on attack rates of sticklebacks upon 'swarms' of water fleas (*Daphnia magna*) that were held in glass tubes so that their movement and positioning relative to one another could be controlled and manipulated, Ohguchi (1981) found that stickleback attack rates declined when the number of *Daphnia* was greater, when they were closer together, when they were phenotypically similar and when they were moving either in parallel or perpendicular to each other. Using the same predator-prey system, Ioannou et al. (2008) also found that the attack success of sticklebacks upon swarms of water fleas decreased with increasing group size. Employing neural network modelling, Tosh et al. (2006) tested the idea that increasing prey numbers leads to less accurate neural mapping of prey, increasing the degree of spatial error associated with attacks against individuals in larger groups. They found that the total number of prey to be more important in bringing about this effect than either prey density of the size or the volume that they occupy.

Predators may attempt to overcome the confusion effect by selecting prey that looks or moves differently from the majority of their group mates and which therefore may be easier to track (Krakauer 1995). The disproportionate likelihood of predators attacking individuals that stand out from the rest of the group is known as the oddity effect. Oddity effects have been demonstrated in a number of predator-prey systems. Focussing on predation by largemouth bass (*Micropterus salmoides*) upon shoals of smaller prey fish, Theodorakis (1989) showed that relatively smaller or larger fish were more likely to be captured than would be expected by chance when they formed a minority within their group. Rutz (2012) found that goshawks (*Accipiter gentilis*) selectively predated rare colour morphs of feral pigeon (*Columba livia*) and that doing so had a quantifiable effect upon their fitness, suggesting that targeting of odd individuals is an adaptive strategy for predators. Oddity effects apply not only to morphology and colouration but also to behaviour. When sunfish (*Lepomis macrochirus*) predators were presented with groups of virtual prey projected onto the side of a glass tank, they were less likely to attack prey individuals that were attracted towards and aligned with their near neighbours, and more likely to attempt to eat those that did not coordinate their movement with the rest of the group (Ioannou et al. 2012; see Fig. 4.9). Landeau and Terborgh (1986) found that single silvery minnows (*Hybognathus nuchalis*) were readily captured by predatory largemouth bass but that the predators' overall success fell and time to capture rose when attacking shoals of increasing size, demonstrating a confusion effect. When odd minnows were present within the shoals, the predators were seen to be able to capture both the odd individuals and more of the majority matched fish too. This effect was present in intermediately sized shoals, but absent from larger ones. Interestingly, this suggests that the presence of odd individuals may also increase predation risk for the group as a whole and not just for those which stand out.

Predation pressure then may select strongly against oddity and concomitantly for traits which enhance the confusion effect, including assortment of groups by phenotype, the evolution of colouration or morphology which disrupts the predators' ability to select or track prey and coordinated movement by groups of prey species. It has been suggested that predation pressure may drive preferences for grouping with phenotypically similar conspecifics in some fish species (Hoare and Krause 2003), and a study by Croft et al. (2009a) found that shoals of guppies from high-predation populations tended be more assorted by body length than those from locations where predation pressure was less severe.

4.3.5 Group Defence Against Predators

Groups of animals may be better able to drive away or fight off predators than lone individuals, who might otherwise have to flee or abandon their shelters or breeding sites in order to avoid being captured. One form of communal defence is mobbing. Mobbing, where several animals gather to harass, pursue or attack predators that might threaten them or their young, has been studied most extensively in birds, but is also known from some fishes and mammals (Caro 2005). For example, colonially breeding Antarctic terns (*Sterna vittata*) defend their nests against predatory South Polar skuas (*Catharacta maccormicki*). Measuring predation levels upon artificial nests, Weidinger and Pavel (2013) found that even though the skuas foraged more in areas where terns traditionally nested, total nest losses were no higher within colonies than they were outside them. This suggests that communal defence by the terns is sufficient to offset the costs of predator attraction to colonies. Research into mobbing behaviour in birds suggests that it may rely on cooperation. Pied flycatchers (*Ficedula hypoleuca*) are prepared to aid their neighbours by helping them to

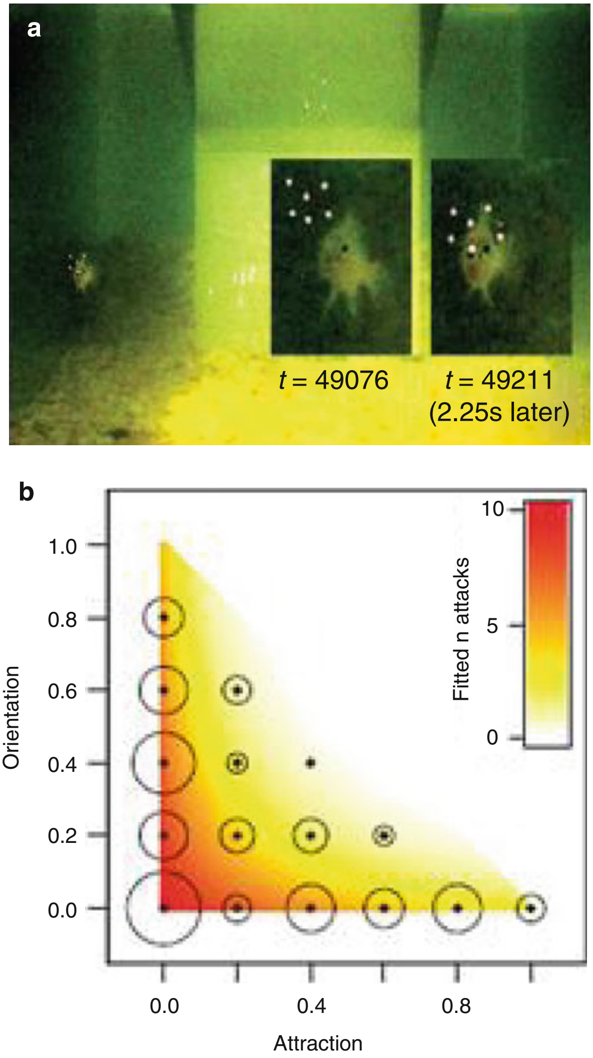


Fig. 4.9 (**a**) A sunfish attacking simulated prey projected onto the wall of an aquarium (*t* corresponds to time frame). (**b**) The effect of the degree to which the prey aligned and orientated with their neighbours upon the number of attacks they received. The size of the *circle* corresponds to the number of attacks received, with prey that were more weekly attracted to and aligned with their neighbours receiving more attacks (From Ioannou et al. (2012))

drive predators away, but their cooperation is a reciprocal arrangement – the birds are far more likely to assist neighbours who have previously helped them in the past (Krams et al. 2008).

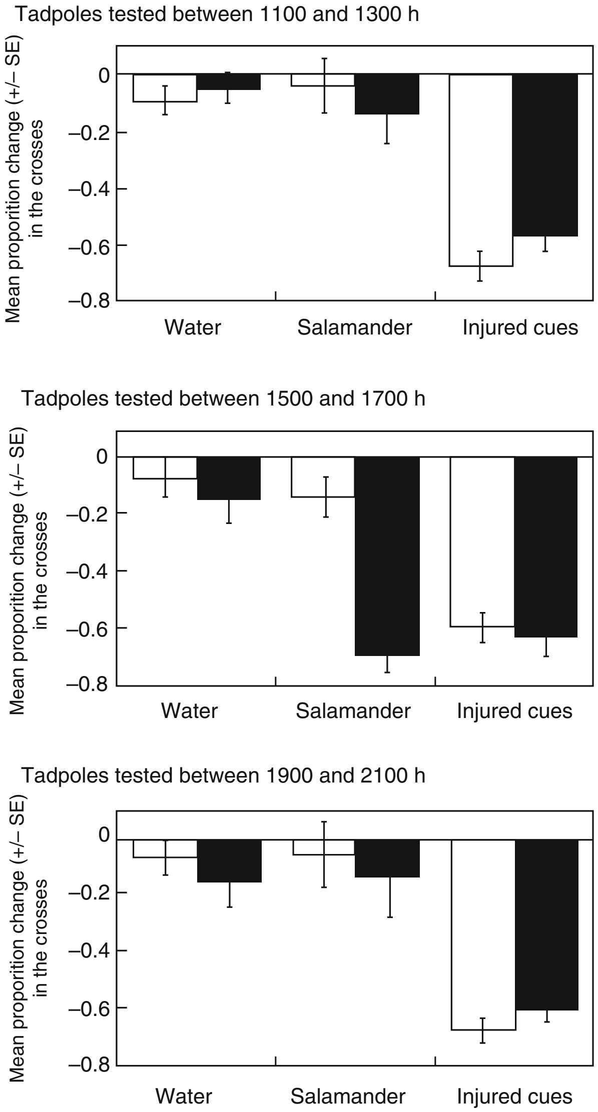
Mobbing may have the immediate effect of driving away the predator, but it may also have other longer term functions too. These may include deterring the predator from launching subsequent attacks or preventing it from gathering information about prey resources, such as the number of nests, eggs or vulnerable young at the location. Finally, group defence may occur among groups of related individuals, where inclusive fitness benefits may select for greater risk taking on the part of defenders who stand to gain from protecting kin (Caro 2005).

4.3.6 Socially Facilitated Learning About Predators

By grouping with others, prey animals might be able to learn about the state, danger posed by or cues associated with different predator types. As discussed above, prey can gather information from others about the arrival or direction of approach of a predator, by responding to changes in their neighbours alertness, orientation or travel direction. Being part of a group might facilitate predator inspection, whereby groups of individuals approach predators, potentially gathering information about their motivation to attack (e.g. Magurran and Higham 1988). This behaviour may function to communicate to ambush predators that they have been detected, which may reduce the likelihood of an attack. It may also allow prey to determine whether the predator is hunting or just resting, which in turn might reduce opportunity costs incurred when prey vacate an area unnecessarily. Beyond this, individuals may learn associations that can provide information during future encounters (Griffin 2004). Young rhesus macaques (*Macaca mulatta*) can learn to fear snakes by seeing others respond fearfully towards them (Mineka and Cook 1988). Indian mynas (*Acridotheres tristis*) inspect novel taxidermic mounts more if they have been presented in conjunction with conspecific alarm calls (Griffin 2008). Tadpoles and even embryos of wood frogs (*Rana sylvatica*) that are exposed to predator chemical cues in conjunction with conspecific injury cues (bodily fluids released from damaged tadpoles, a salient indicator of predator activity) developed stronger antipredator responses compared to those not exposed to these paired cues. Furthermore, they are able to link predation risk to time of day; tadpoles showed stronger antipredator behaviour at the same time of day to which they had been exposed to the predator and conspecific injury cues than they did at earlier or later times (Ferrari and Chivers 2010; see Fig. 4.10).

4.3.7 Predator Learning of Prey Unpalatability

Species that have evolved physical defences, toxins or foul-tasting chemicals that make them unpalatable to predators often advertise this information through conspicuous colouration or ornamentation, a strategy known as aposematism. The evolution of aposematic coloration has been considered something of a paradox, since by being readily detectable, aposematic prey animals might be at risk of harassment, injury or death from naïve predators that have not learned the association between warning coloration and unpalatability (Mappes et al. 2005). Aposematic prey species might be able to reduce this cost by grouping. In grouped aposematic prey, the risk of attack from naïve predators is diluted (Lindström 1999). Groups may also present a stronger warning signal than do lone individuals, facilitating more rapid learning by predators (Gagliardo and Guilford 1993) and perhaps reducing their likelihood of being misidentified as palatable by predators.



Tadpoles tested between 1100 and 1300 h

Tadpoles tested between 1500 and 1700 h

Tadpoles tested between 1900 and 2100 h

Fig. 4.10 Tadpoles that as embryos learned an association between conspecific injury cues (indicative of predator activity, *black bars*) and the odour of a predatory salamander were less active than controls (exposed to water plus salamander odour, *white bars*) when exposed to the odour of the salamander alone, but only at the same time of day to which they were first exposed to the two cues together before hatching. The number of times that they crossed a line drawn across the bottom of a container was taken as a measure of activity and the change in activity relative baseline is shown here. Both groups responded to conspecific injury cues by becoming less active, and neither responded to plain water. These data suggest that not only can tadpoles learn an association between predator odour and predation cues but also that they can learn at what time of the day predators are likely to be active (From Ferrari and Chivers (2010))

4.3.8 A Cost to Prey from Grouping: Area-Restricted Search Tactics by Predators

For predators that are foraging for patchily distributed prey, a productive search strategy may be one that entails travelling through the landscape until they encounter prey, and then focussing further effort in the surrounding area for some time thereafter. Such area-restricted search tactics can increase the likelihood of detecting further members of the prey group. There is good evidence not only that some predators use such a strategy but also that they switch between search strategies in response to prey distribution. Plaice (*Pleuronectes platessa*) search for aggregated prey using area-restricted searches, for example, switching to extended searches characterised by long linear movements with fewer turns when hunting for dispersed prey (Hill et al. 2003). Some predators may integrate not only their own foraging success but also those of others in area-restricted searches; walleye pollock (*Theragra chalcogramma*) quickly join feeding conspecifics when prey are clustered, but show no response to the foraging behaviour of others if prey are spread out (Ryer and Olla 1995).

A number of studies have used the spacing of bird nests, both artificial and natural, in order to quantify the impact of predator area-restricted search tactics upon prey mortality. In one such study, carrion crows (*Corvus corone*) were allowed to forage for artificially camouflaged chicken (*Gallus gallus*) eggs. Eggs were arranged in plots in which they were clustered or dispersed, and each plot contained a conspicuous attractor egg that was readily detectable to the crows. The camouflaged eggs in the clustered plots suffered higher predation that did those in the dispersed plots (Tinbergen et al. 1967). In another study, Sugden and Beyersbergen (1986) focussed on predation by American crows (*Corvus brachyrhynchos*) upon artificial duck nests. When nests were concealed, they were typically not found, but if one nest was exposed, other hidden nests that were nearby were typically also found. In the prairie habitat where these experiments took place cover is patchily distributed which in turn may lead to nest clustering under natural conditions, a factor that may favour such search tactics by nest predators. Other studies, however, have not found a relationship between net spacing and predation levels. Andrén (1991) found that predation on mallard (*Anas platyrhynchos*) nests was not related to the distance of the nearest neighbouring nest, for example, while other researchers have reported the opposite effect, that losses to predation are higher in more dispersed nests (Anderson and Hodum 1993). It is likely that factors besides predation play a significant role in determining nesting density under natural conditions. These may include the need to account for intraspecific competition, risk of cuckoldry, infanticide or parasite transmission. More generally, it would be useful to determine the extent to which more mobile prey are vulnerable to area-restricted search tactics.

4.4 Mixed-Species Groups

While the focus of this chapter has largely been upon single-species groups, mixed-species flocks, herds and schools also frequently occur in nature. Well-studied examples in birds include the parid-dominated mixed-species flocks that form during winter months in temperate Europe and North America (Morse 1970; Dolby and Grubb 1998; Farine et al. 2012) and the foraging flocks of racket-tailed drongos (*Dicrurus paradiseus*), laughing thrushes (*Garrulax cinereifrons*), orange-billed babblers (*Turdoides rufescens*) and other species seen in Sri Lanka (Satischandra et al. 2007; Goodale et al. 2014). Mixed-species groups are common among mammals too, occurring frequently among some primates and dolphins (Stensland et al. 2003) and between wildebeest (*Connochaetes taurinus*) and other herbivores, particularly plains zebra (*Equus burchelli*) (Sinclair 1985). Hoare et al. (2000a, b) described mixed-species shoals of fish consisting predominantly of banded killifish (*Fundulus diaphanous*), and smaller numbers of golden shiner (*Notemigonus crysoleucas*), white sucker (*Catostomus commersoni*) and three- and fourspine sticklebacks (*Gasterosteus aculeatus* and *Apeltes quadracus*). Typically, mixed-species groups consist of one or a few core species which make up the majority of group and a number of minority satellite species. Groups may exhibit local structure; in some mixed-species bird flocks, species that are exploiting different food resources forage at different heights, for example (Sridhar et al. 2009). In other cases, species may sort themselves to some degree within the group. In corvid flocks, rooks (*Corvus frugilegus*) tend to lead, jackdaws (*Corvus monedula*) group most closely with one another, while mated pairs of both species tended to associate as near neighbours (Jolles et al. 2013). Other factors may influence the structure of mixed-species groups too. Swimming speed may passively influence fish shoal structure, and given that swimming speed varies as a function of both species and body length, this may generate a degree of phenotypic assortment such that the body size of different species may vary within groups (Krause et al. 2005).

Both predation and foraging have been suggested to play a role in driving mixed-species grouping. It may pay vulnerable species to associate with others that are better able to detect predators or which produce alarm or warning calls that indicate a predator's approach (Sullivan 1984; Goodale et al. 2014). More generally, animals might be able to form larger groups by joining other species than they otherwise could if they associated with conspecifics only. In such larger groups general anti-predatory benefits such as the many-eyes effect and enhanced attack dilution might apply more strongly. There are likely to be disadvantages, in terms of predation risk, to being in mixed-species groups too. These probably will apply unequally to different species. Certain species, such as odd, minority species, or more conspicuous ones, might be disproportionately more likely to be targeted. Slower or less agile species may be more likely to be captured. Such effects apply to mixed herds of Thomson's and Grant's gazelles (*Gazella thomsoni* and *G. granti*); cheetahs (*Acinonyx jubatus*) tend to avoid numerically larger groups, but when they do attack they are more likely to target the smaller Thomson's gazelle (Fitzgibbon 1990). The presence of certain conspicuous species might make groups more likely to be detected by predators in the first place, and mixed-species groups may receive more attacks than single-species groups, as has been seen in mixed-phenotype single-species groups (Landeau and Terborgh 1986). In some situations, vulnerable group members may overcome predation-related costs by leaving the group if in imminent danger. In mixed-species shoals of striped parrotfish (*Scarus iserti*), stoplight parrotfish (*Sparisoma viride*) and ocean surgeonfish (*Acanthurus bahianus*), the numerically dominant striped parrotfish and minority surgeonfish remain grouped when predators approach, while minority stoplight parrotfishes tend to quit the group and hide among coral (Wolf 1985).

Foraging benefits of mixed-species grouping may relate to relaxed competition; if different species exploit different food resources, then competition levels may be lower than would occur in an equivalently sized conspecific group. Where different species do exploit the same resources, one may benefit from the others ability to find or capture food more effectively. If one species is competitively superior then it may be better able to dominate another species, enjoying greater advantage than it might if it competed solely with conspecifics. As with predation then, there are likely to be costs associated with mixed-species grouping, and these are most often likely to be unevenly distributed between member species. In some cases, members of one species within a mixed-species group might benefit from another species making food available to them that they otherwise could not access. The apparently cooperative hunting behaviour of two fish species in the Red Sea is a relevant example. Here, a giant moray eel (*Gymnothorax javanicus*) is recruited by a roving coralgrouper (*Plectropomus pessuliferus*) to a joint hunt (Bshary et al. 2006). The complementary hunting techniques of the two species mean that both benefit from the alliance. Other, albeit more commensal, examples of this might instances where one species flushes out prey, such as resting insects, as they pass through undergrowth, or disturbing the substrate, or opening up or breaking down structures such as logs or carcasses enabling others to access food within them. Whether the species that engage in these types of ecological interactions could be regarded as being in social groups as we define the term is debateable.

Mixed-species groups may persist in the face of unevenly distributed costs because separate species are able trade-off between these and other benefits. The cost of reduced food intake through competition with another species may be offset if that species is more vigilant and provides useful information about the approach of predators. Satischandra et al. (2007) studied the behaviour of racket-tailed drongos as they flocked with laughing thrushes and orange-billed babblers. The drongos seldom kleptoparasitised these species and instead fed upon insect that they flushed as they moved through the environment. The drongos adjusted their perching height depending upon which species they foraged with, in order to capitalise upon this food source. Satischandra et al. (2007) argue then that the drongos are commensal feeders, exacting little competitive cost upon the species with which they flock. In fact these species may benefit from being joined by drongos, by being able to use and respond to their alarm calls (Goodale et al. 2014). More generally, comparative and meta-analyses by Sridhar et al. (2009) revealed that the bird species that join others to form mixed-species flocks have higher foraging rates than they do when they are in conspecific flocks, while both the joiner and joined species benefit from reduced vigilance costs. Their data suggest that joiner diets tend to consist of insects to a greater degree than those of the joined species and that joiners tend to forage in higher strata. This again might suggest a degree of commensal feeding upon flushed insects, rather than competitive, exploitation of heterospecifics. Instead, they suggest that mixed-species flocking may be driven to a large extent by vulnerable species exploiting the vigilance of heterospecifics so as to minimise their own investment in scanning for predators and maximise their foraging opportunities. Mutualistic mixed-species grouping is expected to evolve where benefits to participating species outweigh costs, even if the benefits (and costs) to each species are not the same. In other cases, exploitative mixed-species groups may occur, where a first species exacts a cost upon a second, but where the second cannot exclude it from the group.

Farine et al. (2012) used a social network approach to test several predictions about the relationship between competitive dominance and interspecific interactions in a mixed-species flock dominated by blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*), with lower numbers of marsh tits (*Poecile palustris*), coal tits (*Parus ater*) and nuthatches (*Sitta europaea*). Specifically, they tested the idea that larger, more dominant species would associate with more individuals, benefiting from the added protection from predators and potential access to social information, while being better able to overcome competition-related costs of being in a larger group. They also investigated whether subdominant species would be more likely to flock with smaller heterospecifics that they would be dominant to. They found support for the first idea, larger and more dominant species had more associates, but none for the second, with smaller and larger birds being just as likely to associate with heterospecifics.

4.5 Summary

Foraging with others brings a range of costs and benefits. Competition is one such cost, and for many group-living species, it is likely to be a major one. It can be direct, as individuals scramble to consume a share of a depletable resource or to aggressively contest ownership of items of food. It can take indirect and subtle forms too; individuals may suffer reduced foraging efficiency as they look out for competitors, avoid depleted ground or because their group mates have alerted prey to their presence, sending it into refuge. Benefits include access to information about the distribution and quality of resources, the opportunity to tackle large or dangerous prey as part of a group and the potential to defend it from rivals. As prey themselves, group-living animals may benefit from a range of effects relating to predator detection and recognition, diluted risk of being targeted or captured and predator confusion, and in some cases groups may be able to repel predators. On the other hand, predators may be more likely to detect or more likely to attack larger groups, and grouped prey might be more vulnerable to the area-limited search tactics used by some predators. Many species are both predators and prey, and their social lives are shaped by the complex interplay between these factors.

Other Benefits and Costs of Grouping

5

5.1 Introduction

The preceding chapter focused upon foraging and predator-prey interactions through the lens of group living. Arguably, these represent the key areas where animals obtain benefits – principally access to information and protection from predators – and pay costs, mainly relating to competition for resources, from grouping with others. This may be so, but there are many other advantages and disadvantages that also apply to social species. Some of these are summarised in this chapter. We have arranged these into broad functional categories, summarised in Table 5.1.

In many of these cases, cost or benefit may depend upon one's point of view. In the context of communal breeding, for example, extra-pair copulations and any subsequent misdirected parental care resulting in investment in someone else's offspring are obvious costs to the cuckold, but are beneficial to the fitness of the individual that is able to breed with more partners, select the fittest mates and secure additional support for its offspring. In some systems, individuals may be simultaneously the victim and the beneficiary. This serves to illustrate that costs and benefits can apply differently to different individuals and may even apply at the same time. Moreover, under natural conditions group-living animals are likely to be subject to multiple costs and benefits across a range of different contexts. Groups of fish that save energy by travelling in schools might also deplete food patches more rapidly. Aggregations of caterpillars might minimise their rate of water loss, but may suffer higher mortality through predation because of the area-restricted search tactics used by their predators. Group living therefore reflects a trade-off between these often dynamic costs and benefits.

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Table 5.1 Contexts in which group-living animals can obtain benefits and incur costs

Section	Category	Benefits and costs
5.2	Cooperative interactions	Opportunities for kin selection Opportunities for cooperation among non-kin
5.3	Courtship and breeding	Access, choice and mating with many partners Benefits (and costs) derived from the formation of leks Opportunities for extra-pair breeding Opportunities for females to avoid harassment
5.4	Rearing young	Communal defence Misdirected parental care Other costs: kidnapping, cannibalism and infanticide
5.5	Developmental costs (Discussed in more detail in Chap. 9)	Ontogenetic costs associated with growing up in a group
5.6	Homeostatic and physiological factors (Discussed in more detail in Chap. 6)	Minimising heat loss Minimising water loss Oxygen depletion
5.7	Pathogens and parasites	Transmission of pathogens and parasites Opportunities to reduce parasite loads through allogrooming
5.8	Travelling together (Discussed in more detail in Chap. 6)	Opportunities for saving energy Mechanisms leading to more effective navigation

5.2 Cooperative Interactions

5.2.1 Kin Selection

Kin selection occurs when individuals perform actions that increase the reproductive success of close relatives. This can occur even if the act performed decreases the direct fitness of the individual performing it, so long as it gains a net indirect fitness benefits from helping its relative, with whom it shares a certain proportion of its genes. The concept was formalised by Hamilton (1964) as $rB > C$, where r is the genetic relatedness of the beneficiary of the act to the individual performing it, B is the fitness benefit gained by the beneficiary of the act, and C is the cost of the act to the performer. In other words, a kin-selecting behaviour is expected to be favoured if the inclusive fitness gains to the performer exceed the direct fitness costs of carrying it out. The term kin selection was introduced by John Maynard Smith in the same year (Maynard Smith 1964).

Kin selection may be a significant factor driving the evolution of cooperative breeding in some species. Typical kin-structured cooperative breeding groups comprise a pair of dominant breeding adults and number of others, often adult or subadult offspring of the breeders. These may fulfil a number of roles, including alloparenting, territory defence and looking out for and deterring predators or brood parasites. Cooperative breeding may be favoured in marginal environments, where breeding pairs might struggle to successfully raise young without help. The breeding pair gain direct fitness benefits, while the helpers, if related to the breeding pair, benefit indirectly, via the reproductive success of their parents. Where helpers are unrelated to the breeding pair indirect fitness benefits are absent. Instead, they may benefit from extra-pair breeding opportunities with one of the dominant pairs, the opportunity to replace one of the dominants or to take over the territory, or they may gain protection from predators or other territory holders by being in the group. Conflict over the control of breeding opportunities between the dominants and the subordinate helpers can incur costs to both parties (Emlen 1984; Clutton-Brock 2002).

Kin selection may occur in other contexts too. Reduced competition may be favoured amongst groups of related foragers for example, since the costs of reduced food intake may be offset by the benefits to relatives. Within sparrow (*Passer domesticus*) flocks, males used aggressive scrounging less frequently towards kin. Related males were less likely to feed from the same patch than were unrelated flock mates, suggesting lower levels of scrounging more generally, while females were more likely to join relatives (Tóth, et al. 2009).

On the other hand, grouping with kin can be detrimental to fitness if it increases the likelihood of inbreeding and inbreeding depression, while in groups where resources are sufficiently scarce that competition between members is severe, related individuals can suffer both direct and indirect fitness costs by exploiting the same resources. Here, we might expect kin to avoid one another (Gandon 1999). In the Lake Eacham rainbowfish (*Melanotaenia eachamensis*), both males and females preferred to associate with same-sex shoals of relatives, while females avoided shoals containing related males, potentially to avoid the costs of inbreeding (Arnold 2000). In zebra fish (*Danio rerio*), juveniles prefer to shoal with kin, while adult females avoid related males. Males choosing between shoals of related and unrelated females showed no preference for either (Gerlach and Lysiak 2006). This is consistent with the idea that nonbreeding juveniles can gain inclusive fitness benefits by shoaling with kin (for example through reduced competition for food), while adult females trade off this advantage against the costs of inbreeding.

5.2.2 Reciprocation

Reciprocal altruism occurs when a first individual performs an action at some fitness cost to itself that causes the fitness of a second individual to be increased, with the expectation that the second individual will perform a similar act, incrementing the fitness of the first, at some point in the future (Trivers 1971). In order for reciprocal altruism to evolve, several conditions are required. Individuals must interact multiple times, they must be able to recognise one another, they must be able to recall the outcomes of past interactions, and they must have the capacity to modify their behaviour in subsequent interactions, depending upon the outcome of previous ones. In a tournament in which multiple different cooperative strategies were pitted against one another, Axelrod and Hamilton (1981) found that the strategy tit-for-tat was the most effective. Tit-for-tat is a reciprocal strategy in which interacting agents either cooperate with their opponent or defect against them, matching the action that their opponent deployed against them in the previous round. Of all the competing strategies, tit-for-tat was the only one that was evolutionarily stable and could not be displaced from the population by anything more effective. Could animal groups provide the necessary conditions for conditional reciprocal altruism to evolve among conspecifics?

Blood-feeding vampire bats (*Desmodus rotundus*) roost communally. They risk starvation if they fail to feed at least every third night, and successful bats have been shown to regurgitate blood to feed those that have not been able to consume blood (Wilkinson 1984). Here, wild bats reciprocally shared blood with kin and with unrelated long-term roost mates in their natural roosts. In the laboratory, testing unrelated bats taken from two roosts, individuals were also seen to feed hungry, unsuccessful foragers; here the majority of feedings occurred between familiar roost mates. In a follow-up study, Carter and Wilkinson (2013) showed that most feedings were initiated by the donor rather than the recipient, ruling out harassment as the main reason for blood sharing. The greatest predictor of blood sharing occurring between a dyad of bats was whether or not the donor had previously received blood from the recipient. This explained a substantially greater proportion of sharing than did relatedness. Still lacking in this system is the demonstration that potential donors withhold blood from those that have previously withheld from them, that is, that they punish defectors. Further research is needed to determine if and how donors respond to defection.

Studying allonursing in reindeer (*Rangifer tarandus*), Engelhardt et al. (2015) found evidence of reciprocal allonursing at the group level, across bouts and within interacting pairs of mothers, with some dyads engaging in more reciprocated bouts than others. Allonursing patterns were not explained by relatedness between mothers, nor were they linked to the rank structure of the group. No evidence of conditional reciprocation, where females punish each other by withholding milk from calves whose mothers had previously refused to feed their young, was seen however. The authors argue that this behaviour can be seen within the context of a market in which allonursing bouts are traded between mothers.

Predator inspection is a behaviour in which one or more individuals approach a predator that they have detected nearby. It may function to allow potential prey to assess the state of the predator, whether it is hunting or not, which might benefit the inspectors by preventing them from incurring the opportunity costs of fleeing the area unnecessarily if the predator poses no threat. Another function of inspection behaviour may be to communicate to an ambush predator that it has been detected and that any ambush, reliant upon catching the prey unawares, may be less likely to succeed and therefore not worth initiating. Predator inspection by pairs of inspectors has been considered in the context of reciprocal altruism, because as they approach the predator have the opportunity to cooperate with each other by approaching at the same rate and maintaining the same distance from the predator, a behaviour which incurs some risk, or else one or both can defect, by holding back or retreating. If only one defects, the other is exposed to more risk, since it is now the closest to the predator. Milinski (1987) studied the behaviour of single sticklebacks (*Gasterosteus aculeatus*) as they approached a predator. The stickleback swam next to a mirror that was angled such that it reflected the fish, making it appear as either a coopering partner that swam parallel and kept pace, or a defector, whose path diverged from that of the test subject, leaving advancing inspector increasingly exposed. Sticklebacks paired with a 'cooperating partner' spent twice as long in the half of the arena that was closest to the predator than did those paired with a 'defecting partner'. In a second study, test sticklebacks approached a predator with a live partner, held behind a one-way glass barrier. The partner either always stopped halfway, simulating defection, or else it continued right up to the predator, simulating cooperation. After four cooperating runs, the cooperator now defected too. The test fish travelled closer to the predator when partnered with the defecting former cooperator than it did when partnered with the fish that had always defected. Milinski et al. (1990) suggested that this reflected trust on the part of the test fish, implying that they can recognise and recall the past behaviour of different inspection partners. Similar behaviour was described for predator-inspecting guppies (*Poecilia reticulata*), using similar experimental protocols (Dugatkin 1988; Dugatkin and Alfieri 1991). Other authors have questioned whether these observations truly constitute tit-for-tat interactions between fishes or whether they instead reflect a by-product mutualism (Connor 1996; Stephens et al. 1997). Stephens et al. (1997) argue that inspectors balance orientation and attraction towards the predator, to gather information about it, with orientation and attraction towards their partner, proximity to which provides selfish herd benefits (Hamilton 1971). Inspectors that stop short should therefore cause their partners to halt their advance at a greater distance too. By this account, conditional approaching can be explained without the need to invoke cooperation. Connor (1996) argues that partner preferences should be expected in by-product mutualisms too, since a bolder partner facilitates more opportunity to gather information about the predator than does a shyer partner that does not approach as closely. As such, Connor reinterprets the observations of inspectors preferring non-defecting partners (Milinski et al. 1990; Dugatkin and Alfieri 1991) in terms of preferences for bolder partners. Recent work by Manica and colleagues, though not explicitly concerned with predator inspection, has developed these ideas by focussing upon the dynamics of social feedback between bold and shy partners as they explore their surroundings (Harcourt et al. 2009; Nakayama et al. 2012; Jolles et al. 2014, 2015).

In summary, blood sharing among vampire bats and allonursing in reindeer are behaviours where reciprocity has been confirmed and where kin selection has been ruled out as the main explanatory factor (Wilkinson 1984; Carter and Wilkinson 2013; Engelhardt et al. 2015). Neither of these cases involved punishment of defectors however. In the case of social interactions in predator inspection fishes, there has been debate within the literature over whether the behaviours observed represent tit-for-tat interactions or by-product mutualism (Milinski et al. 1990; Dugatkin and Alfieri 1991; Connor 1996; Stephens et al. 1997). We suggest that further work is required before we can definitively state which is occurring.

5.3 Courtship and Breeding

Beyond the general advantages of grouping with others, such as reduced predation risk, there are other more immediate benefits to being part of a mixed-sex group of sexually receptive conspecifics, including ready access to potential mates and the opportunity to choose among them. Related to the latter of these is the possibility of using social information to identify higher-quality mates, so-called mate choice copying. Individuals may also benefit from mating with larger numbers of partners than they might if all were dispersed, and for pair-forming species, there exists the opportunity for extra-pair copulations. Of course this can be a cost too, if paired with a partner who engages in extra-pair mating. Advertising individuals may gain from being judged against a backdrop of rivals – superior individuals stand out as so against weaker competitors, while those of mediocre quality may be perceived as being of relative good condition if they strategically position themselves among poorer contenders. While these benefits may broadly apply to grouping species, a few species have evolved lekking behaviour, in which males specifically gather to advertise and compete, with females visiting and choosing among them. Some of the costs of courting within a group include competition between the sexes for the best mates, eavesdropping by competitors, the often high degree of skew in mating success seen between rivals and the risk of being on the wrong end of extra-pair copulations and, by extension, in species that provide parental care, of being cuckolded and finally of receiving harassment from prospective partners.

5.3.1 Access, Choice and Mating with Many Partners

A male's lifetime reproductive success is limited by the number of females that he is able to mate with, while a female's is determined by the number of eggs that she can produce. Given this, females are expected to be choosy, selecting mates that will result in the highest-quality offspring, while males are expected to compete among themselves for access to females. First laid out by Angus John Bateman (1948), this idea became known as Bateman's principle.

Groups provide a setting in which females can choose between males and within which males must compete for access to females. Within groups, both males and females have access to social information – information produced by others – that they can use to locate and select between potential mates. Females may observe and copy the mate choices of other females, mating with the males that they see other females mate with (Jennions and Petrie 1997). This may benefit them by allowing them to forego the costs of assessing potential mates themselves. This can be time consuming and may also expose them to costly harassment by males (discussed below). Among guppies, there is evidence that females will selectively copy the mate choices of older (and presumably more experienced) females (Dugatkin and Godin 1993) and even that they will mate with other males with similar phenotypes to those selected by the females they have seen mating

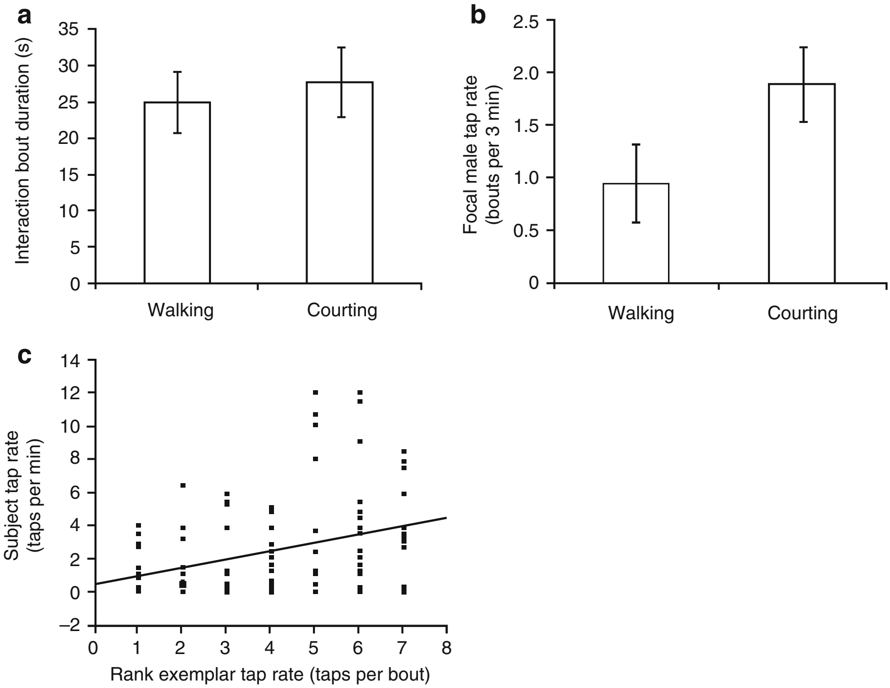

Fig. 5.1 Male wolf spiders were allowed to watch and respond to videos of rival males that were either walking or courting. Test subjects were just as likely to approach, follow and watch courting or walking stimulus males (**a**), but performed more courtship display taps when exposed to courting stimulus males (**b**). The rates of test subject display taps was positively correlated with those of stimulus males whose display rate had been experimentally manipulated (**c**) (From Clark et al. 2012)

(Godin et al. 2005). Non-receptive female guppies may also avoid areas where they see other females being courted, possibly to avoid the costs of being courted themselves (Brooks 1999).

Courting males may exploit the courtship effort put in by their rivals, approaching or loitering close to courting males and attempting to mate with the females that they attract. In some species of chorusing frogs, males begin to call more frequently as females approach. Non-calling satellite males monitor the calling males and can respond by moving towards them, calling themselves in order to intercept the approaching female (Grafe 2005). In the fiddler crab *Uca mjoebergi*, males attract females by conspicuously waving their enlarged claw. Satellite males respond to a courting male by courting themselves, even if the satellite male cannot detect the female directly (Milner et al. 2010). Similarly, male guppies approach and begin to display when they see other males doing so, even if the females they are courting are out of sight (Webster and Laland 2013). When males of the wolf spider *Schizocosa ocreata* are allowed to see videos of males performing courtship displays, they begin to display at rates that match those of their virtual competitor (Clark et al. 2012, Fig. 5.1).

5.3.2 Leks

Leks are groups of males that form specifically for the purpose of courting and mating with females. Competing in close proximity to one another, the males are inspected by visiting females, who may eventually select and mate with one or more of them. Although males may defend small territories on the lekking ground, these typically do not contain resources such as food or nesting materials. Lekking behaviour, its function and evolution have received a substantial amount of attention from researchers, despite it being a relatively uncommon breeding system (Höglund and Alatalo 2014).

By visiting leks, females are able to appraise multiple males, choosing among them to select the best mate. Females may benefit in other ways too. By being able to compare males simultaneously, they may be able to make more accurate decisions about male relative quality than if they were to observe males sequentially, over a longer time period. They may be able to avoid harassment by avoiding lekking males and may be subjected to less harassment outside of the lekking period (but see the hotspot hypothesis, below). They may also benefit from social information provided inadvertently by other females, as they select mates themselves. For males however, the benefits of lekking are less clear. An apparent conundrum relating to leks lies in the fact that mating success within them is highly skewed; typically only a small proportion of the males do the mating, copulating with the majority of the visiting females, while most males do not get to mate at all (Mackenzie et al. 1995). For example, in one study of lekking in the white-bearded manakin (*Manacus manacus*), one male accounted for more than 70% of all mating events (Lill 1974). Why then should males form leks, if only relative few of them appear to benefit from doing so? Several hypotheses have been proposed to explain the evolution of lekking, including the following.

5.3.2.1 Males Gather Where Females Are Locally Abundant

Also known as the hotspot hypothesis, this idea posits that leks should form in areas where females must gather or pass through, for example, when feeding or migrating (Beehler and Foster 1988). Males of the blood-feeding sandfly *Lutzomyia longipalpis* form leks close to hosts, where females come to feed. In a series of experiments, Jones and Quinnell (2002) showed that leks were larger when more hosts were present, female number increased with lek size and female latency to mate was lower in larger leks. Ryder et al. (2006) recorded fruit biomass in multiple lekking areas used by three frugivorous manakin species (*Pipra* sp.) and in non-lek control areas. They found that lekking areas contained more fruit biomass, more ripe fruit and more fruit per plant compared to the controls, suggesting that leks are formed within patchily distributed feeding grounds which females must frequently visit.

5.3.2.2 Groups of Males Are More Easily Detected by Females

Larger groups of displaying males may together present a stronger stimulus than smaller groups or lone males. The benefits in terms of numbers of females attracted must increase at a rate greater than the increase in male group size if individual males are to benefit from this effect alone (Davies et al. 2012). To date as far as we are aware, no compelling evidence for this effect has been discovered.

5.3.2.3 Larger Leks Are Preferred by Females Because They Are Able to Choose Among More Mates

If offspring fitness varies as a function of male quality and females are able to use male traits to assess quality, then females are expected to be discriminated between males when selecting a mate. Given this, females may prefer to mate with males in leks because it allows them to be selective. Females may choose between males on the basis of their ability to defend prime locations within the lek, such as higher or more central points or by assessing their relative quality, on the basis of their size, ornamentation, vigour or condition (Fiske et al. 1998; Davies et al. 2012). In studying female visits and mating behaviour at leks of different sizes the cichlid fish *Nyassachromis microcephalus*, Young et al. (2009) were able to determine that leks were not formed at sites where high female density occurred, nor were they centred around territories held by high-quality males. Instead, they suggest that female choice drives lek formation. Competition between males increased with lek size, while male foraging rates fell. This suggests that holding a position with a larger lek is costly and that females may select males on the basis of their being able to meet the costs of remaining in a larger group.

5.3.2.4 Low-Quality Males Exploit the Success of High-Quality Males

This idea predicts that leks are formed around high-quality males. These are best able to attract females, and lower-quality males attempt to exploit this by gathering nearby and attempting to intercept females as they approach. This is also known as the hotshot hypothesis. While this may be the case in some eavesdropping-communication networks, such as in chorusing frogs (Grafe 2005), the evidence for this effect in explaining lekking is variable. In experiments in which dominant males were removed from leks in both white-bearded manakins (Lill 1974) and sharp-tailed grouse (*Tympanuchus phasianellus*, Rippin and Boag 1974), instead of converging around the next most successful male, as would be predicted by the hotshot hypothesis, the positions previously occupied by the dominant males were instead taken over. In a study of lekking behaviour in little bustard (*Tetrax tetrax*) however, Jiguet and Bretagnolle (2006) found that model birds of different phenotype differed in their attractiveness to females. They found that the phenotype that attracted the greatest number of females also attracted males. They suggest that the hotshot effect is one of several mechanisms underlying lek formation in this species.

5.3.2.5 Lekking Reduces Predation Risk

Males may simply gather together in leks in order to minimise their risk of being preyed upon (see Chap. 4). In some species where male ornamentation or courtship behaviour makes the especially conspicuous, predation risk may be especially high;

however, other species that form leks do not appear to be under severe predation pressure. Reduction of predation risk may not be a common function of lek formation (Davies et al. 2012).

5.3.2.6 Black Hole/Harassment Hypothesis

This hypothesis states that leks form because clustered male territories tend to retain females. Females may benefit from receiving less harassment from outsider males if they are within a cluster of defended male territories compared to if they were to join a lone territory holder or to remain grouped with other females (Stillman et al. 1996). In fallow deer (*Dama dama*), males may benefit from forming clustered territories because even if they lose females to rivals, they can quickly acquire new ones as neighbouring harems are dispersed by competing males. In contrast, lone males that lose harems are less likely to encounter and acquire new females (Clutton-Brock et al. 1992).

5.3.3 Extra-pair Breeding

Breeding in close proximity to others can provide opportunities to mate with multiple partners and potentially to produce additional offspring as a consequence. To males siring additional young, this can be beneficial, while to those males who are outcompeted or whose partner produces young with an outside male, there are clearly costs. These costs may be compounded further if males end up investing care in young that they did not sire themselves. Some males may engage in extra-pair paternity while their partner does too, meaning that they suffer both the benefits and costs. For females there may be a range of benefits in mating with multiple males. These include insurance against infertility in their own partner, maximising genetic diversity among their young, maximising genetic compatibility with their mate, mating with fitter outsiders resulting in fitter offspring and the potential to receive direct benefits such as provisioning for themselves or their offspring from the males that they have mated with (Griffith et al. 2002). A cost of extra-pair paternity to females may be abandonment by a cuckolded mate or his destruction of other male's eggs or young.

Even in nominally monogamous species, extra-pair copulations are common. This has been best studied in birds, where the extent to which extra-pair siring of young occurred initially came as something of a surprise to researchers. Over 90% of birds are thought to be monogamous, and it was initially assumed that breeding therefore occurred more or less exclusively within pairs (Lack 1968). In fact, molecular analysis was to reveal that at least 70% of the bird species that were surveyed produced young that were not fathered by the male member of the pair (Bennett and Owens 2002; Griffith et al. 2002; Westneat and Stewart 2003).

Obtaining a general understanding of the prevalence of promiscuity in birds, in terms of its ecological basis and ultimate fitness benefits, has proved challenging.

Males should be expected to maximise breeding opportunities by mating with other females when the opportunity arises, while females are be expected to breed with higher-quality males, with whom they might produce higher-quality, fitter young (Trivers 1972). Weighed against this is selection acting on male partners not to be cuckolded. In fact, a meta-analysis by Akçay and Roughgarden (2007) reported that genetic benefits for extra-pair paternity were not strongly supported in birds. An earlier review by Griffith et al. (2002) found that interspecific variation in life history, parental care and opportunity to engage in promiscuity could account for some of the variation in extra-pair paternity seen between species, but that data supporting functions of extra-pair paternity were sparse. Here, these authors review a number of studies that had been published that provided evidence for females performing extra-pair mating with mates of higher quality than their partner (the good genes hypothesis) or with those that might provide better genetic compatibility (Griffith et al. 2002), though they note that it is yet to be shown how generally these explanations apply.

5.3.4 Harassment

Unwanted attention from males can be a significant problem for unreceptive females. Males may coerce females into mating, circumventing female mate choice, or else they may attack and injure them if they do not cooperate. Harassment may be costly in other ways too; females that have to deflect male attention may pay opportunity costs in terms of reduced foraging efficiency and vigilance for predators. Conspicuous courtship behaviour by males may even serve to attract predators under some circumstances. Male coercion and female's responses to these – behavioural, physiological and anatomical – can become linked together in evolutionary arms races (Clutton-Brock and Parker 1995). Perhaps the most striking example of such an arms race is seen in the coevolution between male and female genitalia in some waterfowl. Here, males have evolved pseudo-penises that when erected spiral anti-clockwise from their bodies, in order to penetrate the female's cloaca and force inseminations. In response, females have evolved elaborate vaginal morphology, including clockwise-spiralling vaginal tracts with diversions, making it hard for the male's pseudo-penis to achieve full penetration or else shunting it into dead ends (Brennan et al. 2007).

Male courtship and coercive behaviour have been studied extensively in guppies, where various impacts of male harassment upon females have been documented (Darden and Croft 2008; Darden et al. 2009). Here, courtship can increase predation upon females, since while the conspicuous colouration and displays of males makes them more likely to be seen by predators over greater distance, once these get within striking range, it is the larger females that are more likely to be preyed upon (Pocklington and Dill 1995). Harassed females also forage with far less efficiency (Magurran and Seghers 1994). Finally, as well as courting, males also perform forced copulations that undermine female mate choice (Matthews and Magurran 2000).

5.4 Rearing Young

5.4.1 Communal Defence

Animals that rear young together can benefit from group defence against predators and brood parasites. Among birds, more than 10% of species are colonial breeders, rising to more than 90% in seabirds (Danchin and Wagner 1997). In at least some of these species, colonialism might arise primarily through scarcity of suitable nesting grounds, such as cliffs or small islands or offshore outcrops that are free of terrestrial predators. Colonial breeding animals can benefit from the antipredator benefits described in Chap. 4, such as the many-eyes effect and dilution of risk. Synchronised breeding may also lead to predator swamping during the period in which dependant eggs or young are vulnerable.

Colonial and communal breeders may also benefit from active group defence, allowing them to defend young from predators, brood parasites or infanticidal males. Mobbing of predators can have a number of functions. Immediate potential effects may include killing, injuring or driving away predators, deterring repulsed predators from returning, communicating to ambush predators that they have been detected and have lost the element of surprise and attracting larger predators that may prey upon the original predator. Indirect benefits may include communicating to nearby kin that predators are active in the area and communicating to offspring that they should cease begging and/or hide (Caro 2005). Communal breeding can be an effective defence against brood parasites too, and brood parasitism may play a significant role in driving the evolution of communal breeding. Feeney et al. (2013) reported that host defence against brood parasites was more effective in communally breeding songbirds, while on the other hand, the developing offspring of brood parasites did better if they were raised by communal breeding hosts.

5.4.2 Misdirected Parental Care

Extra-pair breeding, discussed above, can be either an advantage, in terms of enhanced fitness, or a disadvantage, in terms of misdirected parental care, from the perspective of the sire or the cuckolded male, respectively. From the female perspective, extra-pair breeding by her partner may be detrimental if it results in him providing care to additional young at the expense of her own offspring. Female promiscuity and resulting uncertainty over paternity can be costly if her own partner abandons her, but can be advantageous if it prevents caregiving males from deserting, induces extra-pair males to provide care (Westneat et al. 1990) or minimises the risk of infanticide by newly dominant males (Hrdy 1980; Agrell et al. 1998).

5.4.3 Other Costs: Stealing of Young, Cannibalism and Infanticide

Kidnapping occurs when young are taken from their nest, parents or group by members of another group. Such behaviour is not widely documented, but may occur for a variety of reasons. In situations where members of larger groups have greater fitness, because they are better able to defend territories or communally rear young, for example, young from other groups may be brought in order to augment group numbers (Kokko et al. 2001). Such a function has been suggested for kidnapping behaviour seen in white winged choughs (*Corcorax melanorhamphos*) and mongooses (*Mungus mungo*) (Heinsohn 1991; Müller and Bell 2009).

By adding additional, unrelated young to their broods, parents may dilute the risk of their own young being preyed upon. In the convict cichlid (*Amatitlania nigrofasciata*), both sexes provide parental care. Broods often contain foreign fry, though parents typically only admit fry that are smaller than their own, possibly because these are less likely to outcompete their own offspring (Wisenden and Keenleyside 1992). It is not clear in this system whether the young are actively kidnapped or whether they are strays that have been adopted.

Finally, kidnapping may also occur as a by-product of hormone actions. In emperor penguins (*Aptenodytes forsteri*), males that have lost their own chick sometimes kidnap their neighbour's offspring. Angelier et al. (2006) suggest that this may be due to high residual prolactin levels and demonstrate that males with experimentally suppressed prolactin levels are less likely to abduct chicks from their colony mates than are controls. It is conceivable that under some circumstances, losing young to kidnappers may not necessarily be costly to parents' fitness, if, for example, the likelihood of survival of the young is not lower than if it had not been taken or if the parent's future fitness does not rely on retaining young within the natal group for communal breeding or defence purposes.

The eggs and young of communal breeders may, in some species and under certain conditions, be vulnerable to cannibalism. Adults may practise cannibalism if foraging opportunities are limited, if it reduces competition for their own young, or simply because the young of other parents represent a cheap energy source. In species that practise filial cannibalism, eating the progeny of others might occur before they pursue the last resort of eating their own young. Cannibalism is very likely to lead to conflict between colony members and, if practised unchecked, could reduce the fitness returns of breeding in groups to the point where it is no longer an adaptive strategy to do so. If the antipredator and other benefits of breeding or raising young communally outweigh the costs of foregoing cannibalism, then this might serve to suppress it. Colony members may still be expected to practise cannibalism at low levels and may also be expected to increase the rate at which they do so if collecting enough food for themselves and their own young through conventional foraging becomes too costly. This is reported for colonies of glaucous-winged gulls

(*Larus glaucescens*) and hybrids of these and western gulls (*L. occidentalis*), where the frequency with which adults prey upon the eggs of other pairs rises with increasing sea surface temperature and the corresponding reduction in prey availability (Hayward et al. 2014). Eggs and young may be at risk of being eaten by other juveniles too, which may practise cannibalism in order to compensate for limited or declining parental provisioning, because they are inexperienced in foraging, or to build up energy reserves before dispersing. As a cost of communal breeding, cannibalism by older juveniles upon younger ones may only come into play towards the end of the breeding period, and as such, it may not significantly affect the majority of breeders, only affecting late breeders, and conceivably may even increase the fitness of parents if their offspring are able to attain better condition and greater survival prospects by doing so. Cannibalism by fledglings is a major cause of nestling mortality in black-crowned night herons (*Nycticorax nycticorax*) (Riehl 2006).

Among social animals, infanticide by males may be selected for if it brings otherwise unreceptive females into oestrous. This may occur especially in groups where one or a minority of males dominate breeding opportunities with female group members. When these males are ousted either from within the group or by outsiders, the offspring they sired are at risk of being killed. This represents a significant cost to the female, and accordingly, they have evolved a number of counter-strategies. These include leaving the group until their young are independent, engaging in multiple mating, making paternity difficult to accurately ascertain and male deception via false oestrous (Packer and Pusey 1983; Agrell et al. 1998). Some rodents have evolved the ability to abort and reabsorb unborn young, known as the Bruce effect (Bruce 1959).

5.5 Developmental Costs of Group Living

Few studies have looked at the effects of living in groups upon development in phenotypically plastic species. Gonda et al. (2009) found that ninespine sticklebacks (*Pungitius pungitius*) that were reared alone developed larger brains than those reared in groups. Moreover, there were differences in brain region size, with those brain regions associated with olfaction being larger and regions associated with vision being smaller, in the fish that were raised alone. This effect was only seen in pond populations and not in marine populations, suggesting that brain plasticity is selected for in some environments but not in others. Beyond these brain size differences, fish from these populations attained a smaller body size over all when reared in groups, even though the food ration available to individual fish was held constant between treatments (Herczeg et al. 2009). These results suggest that for pond populations, which compete more intensively for food than do marine fish (Herczeg et al. 2009), grouping with others can substantially affect growth and brain development. Speculating upon the observation that different brain regions differed in size between single- and group-reared fish, Gonda et al. (2009) suggest that exposure to visual conspecific cues might drive the development of brain regions associated with vision. Given that neural tissue is thought to be expensive to develop and maintain, there may be a trade-off associated with developmental plasticity, with expansion of one brain region necessitating restricted growth in others. We return to the topic of development Chap. 9.

5.6 Homeostatic and Physiological Factors

5.6.1 Minimising Heat Loss

Animals that group closely together may benefit from decreased loss of heat or moisture, by reducing the proportion of the surface of their body that is exposed to the air or to wind or precipitation. Endothermic animals might also benefit from the combined body heat of their group mates, which may warm the surrounding air in enclosed burrows, shelters or nesting materials more effectively than that of a single animal (Hayes et al. 1992). A striking example of thermoregulation comes from studies of the huddling behaviour of emperor penguins (*Aptenodytes forsteri*), which incubate eggs over the winter. During this time they are exposed to severely low temperatures while being unable to feed. Maintaining body heat during incubation is therefore energetically costly. The penguins offset these costs by regularly huddling closely with others (Gilbert et al. 2006), which we discuss at greater length in Chap. 6.

Outside of the breeding season, Abert's squirrels (*Sciurus aberti*) nest together in mixed-sex pairs, and paired nesting becomes more common as the outside temperature falls (Edelman and Koprowski 2007). This is consistent with the social thermoregulation hypothesis, which predicts that endothermic species should rest together to reduce individual investment in thermoregulation (Ebensperger 2001). Communal nesting decreases in the breeding season, possibly because selection favours female behaviour that prevents males from circumventing female mate choice and minimises the risk of infanticide (Edelman and Koprowski 2007). Ectothermic animals may also form huddles in some circumstances, particularly in regions such as deserts, where day- and night-time temperatures vary considerably. The aggregations formed by desert night lizards (*Xantusia vigilis*) are known to be important in conserving heat, and these benefits are particularly important to juveniles (Rabosky et al. 2012).

5.6.2 Minimising Water Loss

The need to minimise water loss and prevent desiccation may be a significant factor in driving grouping behaviour in some animals. Newly metamorphosed American toads (*Bufo americanus*) form dense aggregations around pond margins, sometimes even piling up on top of one another. These aggregations appear to have no antipredatory function and are not performed by toads that are not dehydrated. Desiccated toads that grouped together suffered lower weight loss and lower mortality that those that were kept alone, suggesting that this behaviour serves to limit water loss (Heinen 1993). Among caterpillars of the emperor moth (*Imbrasia belina*), rates of water loss of aggregations of a particular size were exceeded by the combined water losses of equivalent numbers of isolated individuals. Furthermore, individuals from aggregations were more likely to survive water loss than were singletons (Klok and Chown 1999). Adults of the bedbug *Cimex lectularius* are resistant to desiccation; however, their first-instar nymphs are more vulnerable and die if exposed to dry air for too long. These are able to survive prolonged periods of without access to water by entering a state of quiescence and clustering together to reduce water loss (Benoit et al. 2007). The laying of egg clusters may, in part, be an adaption to minimise egg loses to desiccation. In the egg cluster-laying butterfly, mortality due to water loss was lowest in denser, multilayered batches (Clark and Faeth 1998). These authors suggest that reducing the chances of egg desiccation may be one function of egg cluster-laying in drier environments, noting that most North American butterfly species lay eggs in clusters, while tropical species typically lay eggs singly or in looser, single-layered masses. Aggregation also may serve to reduce water loss in some species of mammals. Huddles of hibernating Natterer's bats (*Myotis nattereri*) lose almost a third less water per individual than isolated individuals (Boratyński et al. 2015). It should be noted that aggregating does not always reduce water loss in desiccation-prone animals. Grouping had no effect upon desiccation in the limpet *Cellana tramoserica*, for example (Coleman 2010).

5.6.3 Oxygen Depletion

Localised oxygen depletion may be a significant cost of grouping at higher densities in some aquatic animals and may limit the time that individuals are able to remain close to others or in the interior of aggregations. Hypoxia may occur when groups move between areas that differ in their oxygen availability, from uptake of oxygen by the animals themselves or from a combination of these factors. In Antarctic krill (*Euphausia superba*), dense groups may be able to locally deplete oxygen faster than it can be replenished through diffusion, and the structure of krill swarms may therefore be shaped by the trade-off between the antipredator benefits of being within a dense group and the need to avoid hypoxia (Brierley and Cox 2010). While acute hypoxia may be lethal, even moderate hypoxia can affect the physiology and behaviour of aquatic animals in ways that impact upon their fitness. For example, some fishes have been shown to form more dispersed shoals, to reduce the extent to which they react to and coordinate movement with their group mates, which may in turn reduce the effectiveness of collective antipredator responses (Domenici et al. 2007). Some species may move towards surface waters where oxygen concentrations are higher or may gulp air directly at the surface, increasing their vulnerability to predatory birds (Kramer et al. 1983).

5.7 Parasites and Pathogens

Grouping with others can provide the necessary conditions for the transmission of pathogens and parasites between individuals. This may be exacerbated by the physical injuries and stress of agonistic interactions that occur among competing group mates. In extreme cases, the spread of disease or parasites can reduce or eliminate groups or cause them to abandon roosting or breeding areas. On the other hand, group mates may groom one another, removing parasites more effectively than a single animal could do for itself. Ectoparasites and the need to groom one another to remove them may have played a role in driving the evolution of complex social behaviours in some animal societies.

5.7.1 Transmission of Pathogens and Parasites

At the time of writing, white-nose syndrome, caused by the fungus *Geomyces destructans*, is causing serious declines in the populations of several species of colonially roosting bats in eastern North America. Experiments have shown that infections can be transmitted via physical contact in the little brown bat (*Myotis lucifugus*), which may explain its rapid spread through their dense colonies (Lorch et al. 2011). Novel diseases may spread rapidly through dense groups when animals have limited resistance. Furthermore, the susceptibility of animal groups to disease may be affected by external factors that influence grouping dynamics. Simulating the transmission of bovine tuberculosis through groups of African buffalo (*Syncerus caffer*), Cross et al. (2004) found that periods of drought, in which buffalo interaction networks contain more clusters of closely associated individuals, may facilitate greater rates of disease transmission.

Colony size may affect recruitment of new members, who may act as vectors, transmitting pathogens and parasites between colonies. This is the case in cliff swallows (*Petrochelidon pyrrhonota*), where transient birds are more likely to move between larger colonies, bringing with them ectoparasites. Brown and Brown (2004) showed that the higher likelihood of ectoparasites being brought into larger colonies via transient birds was one factor that accounted for the positive correlation between parasite load and colony size in this species. Parasites and pathogens can affect fitness in a number of ways, through mortality, reduced mating success and lower offspring survival (Møller et al. 1990). In colonial breeders, parasite infections and disease outbreaks have been implicated in the abandonment or failure of colonies, demonstrating that large outbreaks can significantly curtail individual fitness in large proportions of the population (Feare 1976; King et al. 1977a, b).

5.7.2 Allogrooming

Many animals groom themselves in order to remove parasites, dirt and debris from their fur, feathers or integument and may invest a significant proportion of their time budget doing so (Cotgreave and Clayton 1994; Stamhuis et al. 1996). In many social species, individuals may groom one another, a behaviour known as allogrooming (Hart and Hart 1992). Among honeybees (*Apis mellifera*), some hive members even act as social grooming specialists (Kolmes 1989; Moore et al. 1995). Allogrooming may be more effective than self-grooming if it allows for the removal of ectoparasites from parts of the body that a self-grooming animal may have difficulty reaching or seeing (Hutchins and Barash 1976; Brooke 1985). Among rockhopper and macaroni penguins (*Eudyptes chrysocome* and *E. chrysolophus*), allogrooming effort was generally directed towards the recipient's neck and head, for example, and a greater proportion of paired birds were tick-free compared to unpaired birds, a difference attributed to the effects of allogrooming by Brook (1985). As well as providing the conditions for greater rates of parasite transmission then, group living can also provide a means for the removal of ectoparasites. So effective are the grooming behaviours and antimicrobial secretions produced by the leaf-cutting ant *Acromyrmex echinatior*, for example, that it has been suggested that living in larger groups might bring a net benefit in terms of disease resistance (Hughes et al. 2002).

Many parasites that are removed by hosts are consumed. Another benefit of grooming, and by extension allogrooming, may be the nutritional reward gained from eating ectoparasites. Little is known about how important parasite consumption is in terms of its contribution to the energy and nutrient intake of the groomer, nor of the potential epidemiological costs of doing so (Johnson et al. 2010). More research in this area would clearly be useful.

Beyond these utilitarian functions, allogrooming has been exapted to play role in a range of other social behaviours, including courtship, bond formation and reconciliation (Møller et al. 1993). The social function of allogrooming has probably been most widely studied in the context of primate societies. Here, allogrooming and mutual grooming have been shown to be involved in the maintenance of dominance hierarchies, partnerships and coalitions, in courtship interactions and as a precursor to sexual interactions (Dunbar 1991; Schino 2001). The social function of allogrooming is thought to be so significant that it has been termed the 'social cement' of primate societies (Jolly 1985). Allogrooming has been shown to reduce stress in several species (Schino et al. 1988; Keverne et al. 1989). It has also been linked to mating; female crab-eating macaque (*M. fascicularis*) are more likely to mate with males who have recently groomed them, suggesting that a grooming-mating market may exist in this species (Gumert 2007, Fig. 5.2).

5.7.3 Costs of Allogrooming

The principle costs of allogrooming relate to reduced vigilance. In impalas (*Aepyceros melampus*), individuals performing allogrooming took longer to respond to an approaching human (an experimental stand in for a predator), than did the individual being groomed, which in turn took longer to respond to the closest impala that was not engaged in an allogrooming interaction (Mooring and Hart 1995).

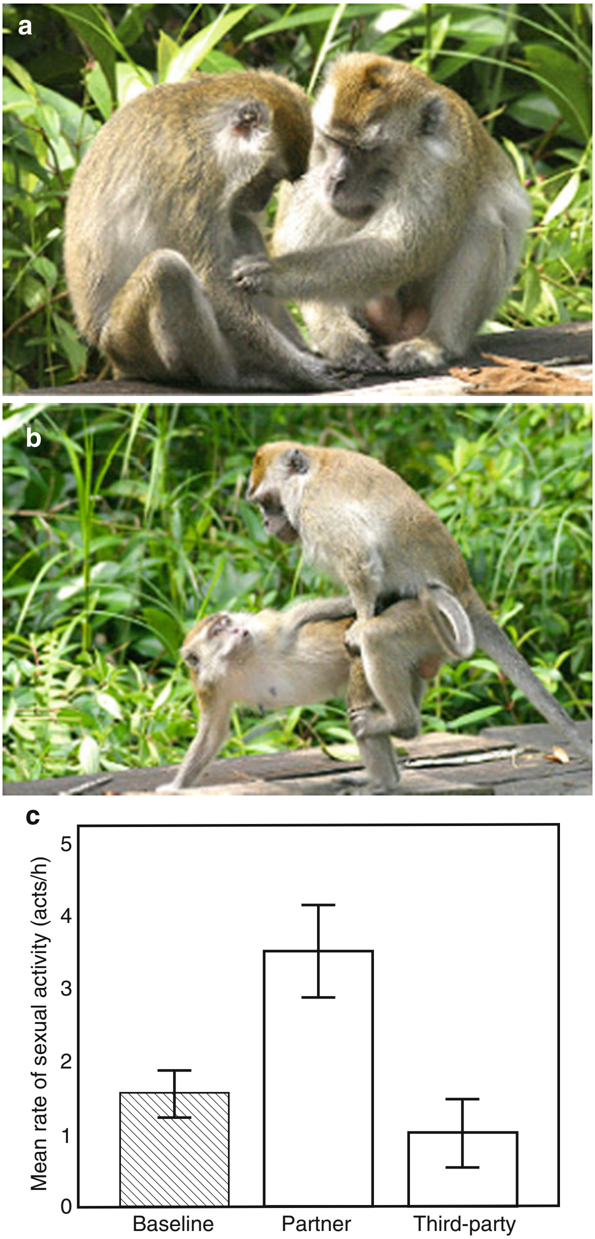

Fig. 5.2 (**a**) Crab-eating macaques engaged in grooming (upper) and mating (lower). (**b**, **c**) Following a grooming bout, females engaged in more sexual activity with their grooming partner than they did before grooming (baseline) and than they did with third-party, non-groomer males (From Gumert 2007)

Allogrooming blue monkeys (*Cercopithecus mitis*) are less vigilant for aerial predators compared to their feeding or foraging group mates, which may translate into greater risk of being preyed upon (Cords 1995). Female rhesus macaques (*Macaca* *mulatta*) that were engaged in allogrooming were less attentive to their infant young, who received more aggression and harassment from their group mates than they did at other times, when their mother was not grooming or being groomed (Maestripieri 1993).

5.8 Travelling Together

5.8.1 Energetic Benefits

Animals can save energy by travelling in groups, by exploiting the wake vortices produced by those travelling ahead of them. Such effects, and the mechanisms behind them, have been described in a number of bird (Fish 1995; Hummel 1995; Weimerskirch et al. 2001; Portugal et al. 2014; Voelkl et al. 2015) and fish species (Herskin and Steffensen 1998; Svendsen et al. 2003; Burgerhout et al. 2013). These are discussed in more detail in Chap. 6, with particular reference to the effect of relative position within the group upon travelling energetics.

5.8.2 Navigation

Animals travelling in groups may benefit from more efficient navigation. This may occur through a number of different mechanisms. For example, naïve animals may be able to follow or acquire information from more experienced individuals that have learned the route already. Similarly, groups may comprise individuals with a diverse range of information, and if they are able to pool this information, all may benefit. Even when they contain no informed individuals, groups may be able to navigate effectively. There are a number of mechanisms by which this may achieved. Individuals may be able to pool their inaccurate estimates about travel direction. While the mean travel direction will come with a margin of error, this is expected to decrease as group size increases, meaning that larger groups will converge upon more accurate travel trajectories. This occurs because the interactions between individuals that allow them to remain together as a cohesive group can also curtail navigation errors that might otherwise lead the group to break up, an effect is known as the many-wrongs principle (Bergman and Donner 1964; Simons 2004; Codling et al. 2007). In some species, groups may make decisions on when to depart and in what direction to travel using quorum sensing and mechanisms analogous to voting. Such mechanisms may allow groups to collectively make travel decisions despite internal conflicts of interest that might otherwise lead to group fragmentation (Conradt and Roper 2005). In other cases still, effective navigation may be achieved through collective sensing, with travel direction emerging from the interaction between individual sensing of environmental gradients and responses to the movements of their neighbours (Berdahl et al. 2013). These ideas are discussed in more detail in Chap. 8, which deals with leadership and collective decision-making.

5.9 Summary

While the primary costs and benefits of grouping for most species relate to foraging and predation (Chap. 4), animals are affected in a range of other ways too. Some of these, such as the advantages and disadvantages relating to courtship and rearing young within a social setting and exposure to diseases and parasites, are likely to apply fairly generally, while others, such as lekking, cooperative interactions, collective heat and water regulation and energy saving through collective travelling, are probably confined to a specialised few species. In Chap. 6 we continue to explore these costs and benefits by looking at how their impact can vary between group members. In Chap. 7 we look at some of the ways in which group members can balance them.

Distributions of Costs and Benefits Within Groups

6

6.1 Introduction

The previous two chapters described how resources and risk affect the costs and benefits that group members obtain from sociality. However, not all group members necessarily obtain the same benefits, nor do all pay the same costs. The net benefit of group membership is typically skewed in favour of some individuals to the detriment of others. In some cases this skew may be extreme, so that it may pay some group members to leave the group, depending on the opportunities available outside the group. More often, however, all members of the group fare better than they might on their own, even if some do better than others. Furthermore, the benefits and costs are not fixed, so that those that obtain relatively low rewards at one point in time may be able to improve their lot subsequently. There are two main predictors of these cost and benefit inequalities within groups: firstly, the position that an animal occupies within a group, relative to other group members, and, secondly, the position an animal occupies within a dominance hierarchy. These factors often interact, with dominant individuals taking up the most favoured positions at the expense of their subordinate social partners. In this chapter, we first examine the payoffs associated with different positions in animal groups; we then examine how animals are able to respond dynamically to these by adjusting their relative position in their group. We discuss the different costs and benefits connected with being dominant or subordinate in a social group hierarchy. Finally, we examine the constraints that animals may face on their ability to take up beneficial spatial positions within groups with particular reference to the existence of dominance hierarchies.

6.2 Position-Related Differences in Costs and Benefits

The spatial positions occupied by individuals in a group are associated with different costs and benefits (Krause 1994). While group members may benefit one another simply by aggregating to form a group, each individual will attempt to position

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itself so that it gains the best possible return from its membership of the group. The spatial position adopted by an animal can best be considered in relation to the positions of other group members. This animal's relative position in the group may affect its risk of predation or parasitism, its rate of nutrient intake, its reproductive success (see Chap. 5 for a discussion on leks) or its energetic costs, primarily through either locomotive efficiency or thermoregulation. In addition, an animal's relative spatial position in its group is determined to an extent by whether the group is stationary (and here we include instances where group members are mobile, but the group as a whole moves at a speed lower than that of its individual members) or whether the group is mobile, that is, group members are polarised and moving in some common direction. Generally speaking, research on animals in stationary groups has focussed on the differences in the costs and benefits of peripheral versus central positions, while in moving groups, animals may additionally occupy positions to the front or the back of the group.

6.2.1 Group Position and Predation Risk

The relationship between the spatial position of an animal and its risk of predation was discussed by Hamilton (1971) as the key element of his selfish herd concept. If predators typically attack those prey animals that they encounter first, then those on the edges of stationary groups are at greater risk than those in the centre. Hamilton proposed that to ameliorate risk, prey animals should strive to move to the centre of groups, thereby 'selfishly' putting other individuals between themselves and the predator. Although intended as a means to explain grouping behaviour in animals, the selfish herd is based on the assumption of greater risk at the edges of groups. Those at the edge may be said to have a greater domain of danger, and they can reduce this domain of danger by moving away from the edge or by moving towards the centre of the group (King et al. 2012).

In practice, this means adopting a movement rule in response to being confronted by some threat (Viscido and Wethey 2002). Hamilton originally proposed that animals under risk might move towards their nearest neighbour in space; however, James and co-workers (2004) offered an alternative to this whereby animals would move towards their nearest neighbour in time, which may be more realistic since it considers the orientation of an animal relative to its neighbours. As group density increases, however, it may be necessary for animals to adopt more complex movement rules if they are to effectively reduce their domain of danger and especially for them to move away from risky peripheral positions; in particular animals need to consider the positions of many group members rather than just a single nearest neighbour (Morrell et al. 2011; see Fig. 6.1).

Studies that have examined the relative risk faced by individuals in different positions tend to support the contention that risk is greatest at the edge of the group relative to the centre in stationary groups. Research on the reproductive success of colonially nesting birds suggests that nests at the periphery suffer more than those at the centre of the colony from predation, despite the greater potential for

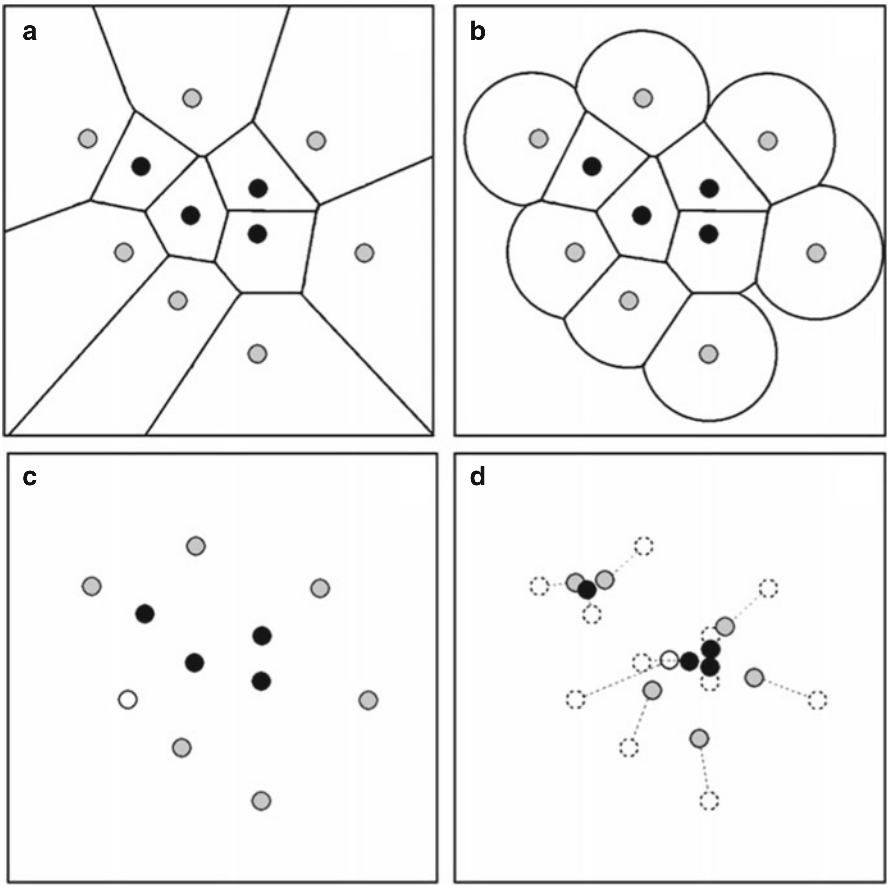


Fig. 6.1 The domains of danger concept is illustrated using Voronoi tessellations. In box (**a**), peripheral individuals have unlimited domains of danger, whereas box (**b**) presents arguably a more realistic case, where the domains of danger are finite or limited. Individuals on the outside of the group (*shaded*) typically have larger domains of danger than individuals in the centre of the group (*black*). From this, we might infer that peripheral individuals face greater danger. Morrell and co-workers (2011) showed that individuals that are able to adopt behavioural rules that take into account the position of multiple neighbours are able to move rapidly from peripheral to central positions. This is exemplified by the movement of a single individual (*clear circle*) from a peripheral position in box (**c**) to a central position in the group at a subsequent time step in box (**d**) (From Morrell et al. (2011))

cannibalism towards the centre of such colonies (Wittenberger and Hunt 1985; Perry et al. 2008; Tenaza 1971; Kruuk 1964). Where it occurs, this risk gradient from edge to centre may be the result of reasons other than the edge nests having a larger domain of danger and can include active predator deterrence by the larger numbers, or densities, of nest defenders towards the centre of a colony (Phillips et al. 1998; Wittenberger and Hunt 1985). The pattern of higher predation on the periphery of colonial breeding birds is not universal, however. A study on least terns

(*Sterna antillarum*) found that the type of predator was important in determining the relative risk of edge versus centre nests. While American crows (*Corvus brachyrhynchos*) preferentially attacked the periphery of the colonies, black-crowned night herons (*Nycticorax nycticorax*) attacked the centre (Brunton 1997).

In the broader context of position-related predation risk in animal groups in general, peripheral individuals do suffer in comparison to those in the centre of the group (although see Parrish 1989). The extent of the risk faced by peripheral individuals varies as a function of the density of the prey group and the type of predator and the distance over which it launches an attack (Hirsch and Morrell 2011; Romey and LaBuda 2010). A study of sticklebacks (*Gasterosteus aculeatus*) preying on stationary aggregations of water fleas (*Bosmina longispina*) showed that per capita risk was substantially greater for those water fleas occupying peripheral positions (Jakobsen and Johnsen 1988). Similarly, Romey and co-workers considered the role of prey group geometry on individual risk in whirligig beetles (*Dineutus discolor*), which form two-dimensional groups, and toad (*Bufo bufo*) tadpoles, which form three-dimensional groups. In each case, peripheral individuals were far more likely to be targeted (Romey et al. 2008). In mobile groups, peripheral individuals remain at risk, but in addition to this, leading individuals may be the first to encounter ambush predators, thereby increasing their individual risk (Bumann et al. 1997; Krause et al. 1998b), whereas pursuit predators may be most likely to pick off stragglers towards the back of a moving group of prey. A complicating factor in making an accurate assessment of the relative risk of different spatial positions, especially in mobile prey groups, is the tendency of some predators to harry the prey, launching attacks or feints with the intention of causing the group to fracture and for individuals to become isolated. In these cases, the position of a prey animal at the point at which the attack begins may have little or no influence on their per capita risk. Furthermore, many studies on position-related costs and benefits to date have failed to consider the effect of prey density on their predation risk (a notable exception to this is the previously mentioned study by Romey and co-workers (2008)). This is an important consideration since some predators are known to target prey that have higher domains of danger (Quinn and Cresswell 2006), in other words, prey animals in less dense parts of the group. Several studies have reported differences between the densities of the edges versus the centres of groups, or between the front and back of groups (Ballerini et al. 2008; Quinn and Cresswell 2006; Hemelrijk and Kunz 2005; Brierley and Cox 2010; Doonan et al. 2003).

As with predation risk, the likelihood of being parasitised may be greater at the edges of groups, especially where the parasite in question actively seeks out its host. Reindeer (*Rangifer tarandus*) are harassed by biting flies and herd formation has been hypothesised as a means to limit exposure to these pests. A study by Helle and Aspi (1992) used different spatial arrangements of artificial animals to mimic the patterns shown by reindeer. They found that peripheral individuals bore the brunt of the attacks by the parasites. Similarly, Stumbo et al. (2012) found that fathead minnows on the periphery of groups were more likely to be infected by trematode parasites. The probability of infestation by parasites such as ticks that rely largely on sit-and-wait tactics to locate a host may be a simple matter of encounter probability. Animals at the front of moving groups, or at the periphery of stationary groups, are

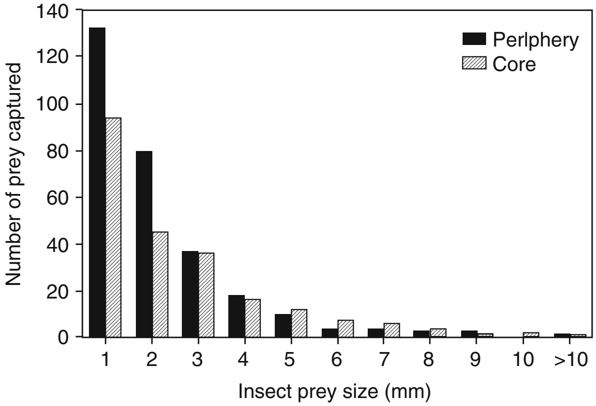


Fig. 6.2 The number of prey captured by webs at the periphery of groups of the colonial spider *Metepeira incrassata* is greater than the number captured by central webs (From Rayor and Uetz (1990))

likely to be the first to encounter the parasites and so may be more likely to be infected. There is limited support for this contention, based on studies of cattle (Newson et al. 1973; Chungu et al. 2001), but much more work needs to be done on this topic if we are to claim a general understanding.

6.2.2 Group Position and Foraging

Differences in the rate and quality of nutrient intake have also been documented according to the relative positions of foragers in a group. The relationship between the costs and benefits of edge versus centre, or front versus back, positions depends on certain characteristics of the food resource (Hirsch 2007). If the food is abundant, it may be that there is little difference in the nutrient intake of animals in different positions. When it is clumped in space, certain individuals in the group may be able to monopolise the resource. This may lead to higher intake rates for more aggressive animals in the centre of a group focussed around a food resource, such as may occur with carnivores at a kill. If food is more evenly distributed, and depletes rapidly, then those that encounter the food first are likely to manage the highest intake rates. For example, those at the edge of stationary or slow-moving groups typically manage higher intake rates than those in the centre, usually because resources are less likely to be depleted and because competition is lower. Barnacle geese (*Branta leucopsis*) at the periphery of groups have a higher rate of intake and also obtain a greater proportion of higher-quality food, in this case clover, compared to more central members of the flock (Black et al. 1992). The same pattern of edge-related foraging benefits has also been reported in mussels (*Mytilus edulis*) and colonial spiders (Okamura 1986; Rayor and Uetz 1990) (see Fig. 6.2). The foraging benefits available to those at the edge of a group may also mean that such individuals are able to forage more efficiently and hence spend less time foraging (Keys and Dugatkin 1990; Petit and Bildstein 1987). Similarly, in moving groups, those at the front have an advantage in foraging, since they encounter food items first and, as a result, consume both a greater number and a higher quality of food items (O'Connell

1972; Krause 1993b). DeBlois and Rose (1996) examined the stomach contents of cod (*Gadus morhua*) in a huge migrating shoal. Their findings supported the prediction of position-related benefits to foraging, with fish towards the front of the group having greater food intake and a greater proportion of preferred prey items in their diet than those towards the back of the group.

6.2.3 Travelling Efficiency in Moving Groups

While differences in predation risk and foraging patterns represent the main determinants of position-related costs and benefits for most species of group-living animals, there are other factors. For example, the energetic costs of locomotion are known to be greater for leading animals than for those that follow them. Drafting, or using the aerodynamic or hydrodynamic advantages of following another's slipstream, is used by many animals but has been studied most extensively in group-living birds and fishes. The tail-beat frequencies of sea bass (*Dicentrarchus labrax*) towards the back of a shoal were 9–23 % lower than those at the front and that tail-beat frequency was positively correlated with oxygen consumption, an indicator of energetic expenditure (Herskin and Steffensen 1998). Similarly, in shoals of roach (*Rutilus rutilus*), fish swimming at the rear of the shoal had tail-beat frequencies around 7–12 % lower than those at the front under a range of different current flow velocities (Svendsen et al. 2003). Groups of eels (*Anguilla anguilla*) swimming against a current required less oxygen per capita and, at higher flow rates, performed fewer tail beats per unit time than singletons. The eels swam in parallel rather than in a procession or diamond-lattice arrangement and may have benefited by exploiting Kármán vortices (Burgerhout et al. 2013). The distribution of fish relative to one another within the shoal does not generally correspond to that predicted to be the most energy efficient, however. This may be due to the need to minimise predation risk, which favours shoal geometry that is suboptimal in terms of travelling efficiency but which enables the shoal members to better detect and avoid approaching predators (Weihs 1973; Abrahams and Colgan 1985).

The V-shaped formations adopted by larger-bodied birds, typically when undertaking long flights, are a familiar sight and have long been supposed to enhance travelling efficiency by reducing energy expenditure for trailing individuals (Hummel 1995; Lissaman and Shollenberger 1970; Bajec and Heppner 2009; see Fig. 6.3). Great white pelicans (*Pelecanus onocrotalus*) flying in formation show reduced wingbeat frequencies and reduced heart rates, which are both indicative of energetic savings (Weimerskirch et al. 2001). In V formations, each bird passes through the upwash field produced at the wingtip of the preceding bird in the formation, reducing the amount of effort required to generate lift. It is because the upwash fields are produced at the wingtips that the birds adopt a V-shaped flock, with following birds laterally offset from the one in front of them. It is thought that smaller birds generate wake patterns that are too variable to be exploited by their flock mates and that this is why V and similar diagonal formations are usually only seen in larger birds, such as geese, ducks, cranes and pelicans (Hummel 1995). The relationship

Fig. 6.3 V formation of snow geese (*Chen hyperborean*) (From Bajec and Heppner (2009))

between flock geometry, individual relative spatial position and flight energetic requirements was examined in detail in a study in which bald ibises (*Geronticus eremita*) equipped with data loggers were shown to move into aerodynamically optimal positions, behind and to the side of the bird immediately in front of them. Doing so allows them to gain lift by exploiting the upwash generated at the wingtip of the preceding bird. Their wingbeats were seen to be spatially in phase, maximising upwash capture. Where the birds flew immediately behind one another in procession, their wingbeats moved into antiphase. This may serve to counter the effects of downwash upon the trailing bird, which would otherwise push it down (Portugal et al. 2014). While the trailing birds gain an advantage in terms of additional lift and lower energetic costs, the lead bird at the apex of the V does not. The ibises solve this problem by taking turns at the front, with individuals spending equal amounts of time in frontmost and trailing positions (Voelkl et al. 2015). But while travelling in groups can yield energetic benefits for larger birds flying in formation, birds flying in the less organised flocks typical of many species, including small passerines, may actually suffer energetic costs of travelling in a group (Usherwood et al. 2011).

Travelling in formations has also been documented in mallard ducklings (*Anas platyrhynchos*). Those that swam in a linear procession used less effort, measured by the length of the arc traced by their feet as they paddled, than did lone ducklings. Much as for the examples discussed above, the rearmost ducklings required less effort to propel themselves than did those at the front of the procession (Fish 1995). Similarly, processions of migrating spiny lobsters (*Panulirus argus*) appear to benefit from reduced drag. Bill and Herrnkind (1976) were able to demonstrate experimentally that the amount of energy required to drag a column of lobsters was less than the sum of the energy costs required to drag the same number of single individuals.

6.2.4 Group Position and the Conservation of Resources

In some cases, aggregating with conspecifics can promote the conservation of resources. One such resource is water and there are many examples of animals reducing their rate of desiccation by forming groups (see Chap. 5). For example, groups of woodlice (*Porcellio scaber*) reduce per capita water loss by more than 50 % compared to when isolated (Broly et al. 2014). Nonetheless, while desiccation is often cited as a benefit of aggregation for intertidal animals such as limpets, evidence suggests that this may not always be the case (Coleman 2010). Intuitively, it seems likely that animals at the periphery of groups benefit less from this than those at the centre; however, this is seldom explicitly tested. There are other cases where dense concentrations of animals cause localised depletion of critical resources. The pattern of oxygen depletion by large swarms of krill is an example of this. The extent of the depletion is greatest in the centre of the swarms; hence, those in the middle of the group suffer relative to conspecifics on the periphery of the group. The movement of the central individuals to the outside of the group in response to the oxygen gradient has the effect of causing large vacuoles to form in the middle of krill swarms (Brierley and Cox 2010; see Chap. 3).

For endothermic animals, grouping with conspecifics can facilitate the conservation of body heat in cold climes (Gilbert et al. 2010). Birds in temperate regions are more likely to form clusters at roosts during winter when temperatures are at their lowest (Armstrong and Whitehouse 1977). In terms of both water and heat conservation examples, intuition suggests that central individuals in a group will benefit considerably more than those on the periphery, but relatively few studies have examined this explicitly. Those studies that have tested this confirm the prediction that central individuals gain a considerable thermal benefit from huddles. For example, Hatchwell and co-workers found that long-tailed tits (*Aegithalos caudatus*) occupying peripheral positions in communal roosts suffer greater loss of mass compared to those in more central positions, indicating that the costs of thermoregulation are not borne equally by all group members (Hatchwell et al. 2009). In other species, individuals may rotate their positions in huddles so that the costs and benefits are more evenly distributed, as occurs in the litters of mammals such as rats and rabbits (Bautista et al. 2008; Alberts 1978). This constant cooperative rotation might be expected among littermates; however, it is also seen among unrelated individuals in species such as emperor penguins (*Aptenodytes forsteri*), where peripheral individuals bear the brunt of the Antarctic conditions, but the positions in the huddle are dynamic, leading to more even sharing of costs and benefits (Gilbert et al. 2006; Zitterbart et al. 2011). The benefits of these huddles for those individuals in the interior may be considerable: Gilbert et al. (2006) found that the ambient temperature within huddles was above 0 °C, peaking at 37.5 °C, even while the air temperature averaged −17 °C (see Fig. 6.4). In some cases, the huddles may even be too effective, causing overheating in central positions and resulting in the huddles splitting.

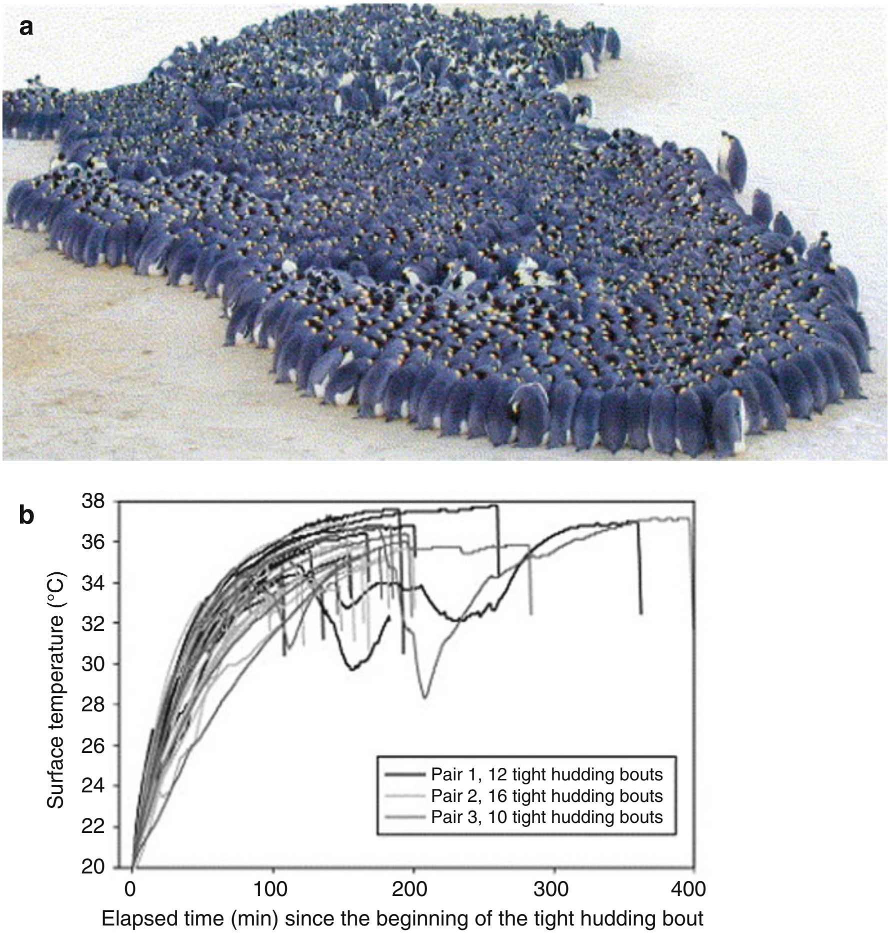


Fig. 6.4 (**a**) A huddle of emperor penguins. (**b**) Increases in temperature over time recorded for pair of penguins engaged in bouts of huddling (From Gilbert et al. (2006))

6.3 Positional Preferences and the Trading-Off of Costs and Benefits

Given the heterogeneity of costs and benefits associated with different positions in groups, it is perhaps unsurprising that individuals respond by expressing preferences. Hamilton predicted that when under threat, animals in stationary groups will attempt to move to the centre of the group, where their domain of danger and hence their per capita risk are usually reduced (Hamilton 1971). Empirical support for this prediction has been supplied by numerous studies. When water fleas are attacked by a predator, they respond by moving towards the centre of their group (Jakobsen and Johnsen 1988). Similarly, Krause applied an ingenious experimental design to examine the positioning behaviour of fish as the perception of risk increased (Krause 1993a). By habituating some shoal members to alarm pheromone (‘Schreckstoff’), while leaving others in their typical state, in which they adopt risk-averse behaviour following their detection of Schreckstoff, Krause was able to test the positional preferences of frightened fish in the absence of interference from other shoal members. Indeed, when Schreckstoff was added to the test arena, non-habituated fish showed a strong preference for central positions in the group.

Behavioural differences have been reported between animals at the margins of groups and those in the centre. Those at the edge have larger domains of danger and so adopt more risk-averse behaviour. For example, ring-tailed coatis (*Nasua nasua*) at the front of a group, or on the periphery of a group, are more vigilant that those in central positions (Di Blanco and Hirsch 2006). Similarly, birds at the edge of a foraging flock of semipalmated sandpipers (*Calidris pusilla*) engaged in less risky, and potentially less rewarding, foraging behaviour than those at the centre (Beauchamp 2013). Animals at the edge of a group may also be more reactive to potential threat. Herbert-Read and co-workers (2015) reported that Pacific blue eyes (*Pseudomugil signifer*) on the periphery of the shoal, and nearest to a simulated predator strike, responded to that strike by dramatically increasing speed, moving away from the threat and overtaking other shoal members. The net effect was that these individuals repositioned themselves, by moving to typically less risky positions in the centre of the group. The expression of behavioural differences between edge and centre or between front and back positions is likely to be more pronounced in circumstances where the animals experience risk or uncertainty. For example, shoals of mosquitofish (*Gambusia holbrooki*) switch leadership far more frequently in an unfamiliar environment than in a familiar one (Burns et al. 2007). This may be a result of a greater need for social feedback in novel environments, so that an animal finding itself at the front of a group in such a situation pauses, allowing those following to catch up and potentially overtake (Swain et al. 2015). Alternatively, it may be that leadership imposes greater cognitive demands than following. An animal at the front of the group has to maintain its vigilance for predators or food patches, while navigating a path and avoiding obstacles (Piyapong et al. 2007). As a result of this, leaders may suffer the cost of having to divide their attention, which in turn may contribute to increased predation risk for leading animals (Dukas and Kamil 2000; Dukas 2002).

While animals perceiving increased risk tend to attempt to move to the centre of groups, hungry animals move in the opposite direction, to the edges or to the front of their group, where foraging opportunities are greater (Krause et al. 1998a). This may occur through hungry animals adopting different interaction rules, for example, showing decreased social attraction towards conspecifics and/or increasing their speed of locomotion (Reebs and Saulnier 1997; Walker et al. 1999; Couzin and Krause 2003). Moving to the front, or to the edges of the group, while beneficial in terms of foraging, can expose a group member to greater danger, so animals have to trade off these foraging benefits against the increased risk of predation. Colonial orb-weaving spiders, *Metepeira incrassata*, show a size gradient across their groups, with the largest individuals in the centre and smaller spiders towards the periphery of the group. Although foraging opportunities are greatest at the edges of the groups, so too is the risk of attack by predators such as hummingbirds, wasps and other spiders. Furthermore, larger spiders are attacked preferentially by predators, which effectively constrain them to the safer central areas of the group. The smallest spiders are competitively inferior to the larger spiders, so they may move to the edges of the group to reduce competition. In moving to the edge, they are exposed to greater risk of predation but gain more foraging opportunities. Those that survive the elevated risk at the edge tend to move towards the group centre as they grow and as their competitive ability improves with size and age (Rayor and Uetz 1990, 1993). Animals at the front of groups have to trade off the foraging benefits against both risk and the higher energetic costs imposed by travelling in these positions (Romey 1995; Romey and Galbraith 2008). The trade-off between risk and reward is affected by the animal's level of satiety – hungry animals may be more likely to accept risk in return for foraging rewards (Romey and Wallace 2007). In an experiment on roach, Krause and co-workers (1992, 1993b) demonstrated that the positions occupied by fish were dynamic and were strongly influenced by hunger. Food-deprived fish moved to the front of the shoals where they were able to monopolise feeding opportunities but fell back into the centre of the group as they became increasingly satiated. Positional preferences are therefore subject to dynamic feedback between satiety, foraging rewards and risk.

6.4 Dominance and the Costs and Benefits of Group Membership

Social animals very often form hierarchies. The establishment and maintenance of a dominance hierarchy is known to reduce aggression within social groups and is predicted to increase the fitness of group members (de Waal and de Waal 1982; Guhl et al. 1945; Lloyd and Rasa 1989; Issa and Edwards 2006). But while a hierarchy may benefit all to a degree, some group members typically benefit more than others. The status that an individual has within its social group may determine, among other things, the access that it has to resources. Those animals that manage to achieve higher positions in the hierarchy tend to obtain greater benefits from their membership of a social group, although the extent to which different individuals within the group realise and can maintain different payoffs is dependent on the strategies employed by dominants and the alternative options available to subordinates (Vehrencamp 1983). For example, high-ranking spotted hyenas (*Crocuta crocuta*) gain greater access to food resources at a kill (Frank 1986). Similarly, dominant dark-eyed juncos (*Junco hyemalis*) in feeding flocks tend to monopolise the best food resources and effectively exclude subordinate birds from their favoured diet choices (Langen and Rabenold 1994). Aside from foraging benefits, dominant individuals may be able to monopolise decision-making, leading to consensus costs for subordinate individuals where they are forced to compromise on their own preferences regarding the timing and direction of group movements (see Chap. 8). The elevated status of dominant individuals within a group, coupled with greater access to resources, tends to translate into greater lifetime fitness than that of subordinate group members (Packer et al. 1995).

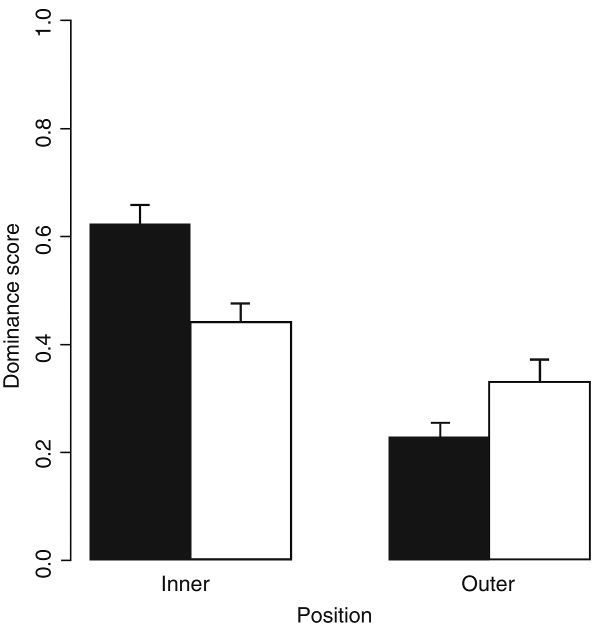
Despite these inequalities, subordinate individuals are predicted to remain as part of the group so long as the benefits of doing so outstrip those of being solitary (Vehrencamp 1983). Where groups are stable and comprise related individuals, the skew in payoffs between dominant and subordinate individuals may be greater than that seen in unrelated groups, particularly when it comes to reproduction. But in these cases, while dominant individuals may suppress the reproduction of lower-ranking animals, the latter still obtain inclusive fitness benefits from remaining with the group and helping to raise offspring to whom they are related. In addition, by remaining with the group under these circumstances rather than dispersing, the subordinates may also improve their status as they age, potentially even becoming reproductive themselves (Kokko and Johnstone 1999).

Despite the fact that dominant animals are able to obtain a greater share of resources than subordinates, and at less of a cost, in some species, the net fitness benefits of being dominant may only be marginally greater than for being subordinate. In some cases the costs of being dominant could even outweigh the benefits in the short term (Rohwer and Ewald 1981). The reason for this can be found in the need for dominant individuals to repeatedly consolidate their position in the face of challenges from rivals, which can involve fighting. As a result, dominant individuals may manifest elevated levels of stress hormones, possibly as a result of challenges made to them by lower-ranking animals (Creel 2001). Even in well-established dominance hierarchies, dominant animals may have higher metabolic rates than group members lower down the hierarchy and hence have greater energy needs (Roskaft et al. 1986; Hogstad 1987; Bryant and Newton 1994). Nonetheless, despite the undoubted existence of some costs to being dominant, dominant individuals typically enjoy greater lifetime fitness (Ekman and Askenmo 1984; Lahti 1998). We discuss the skew of costs and benefits among individuals in the context of group size further in the following chapter.

6.4.1 Dominance and Positioning Behaviour in Groups

Simply having a preference is insufficient to guarantee occupancy of a position in the group. The skew of costs and benefits associated with different positions mean that group members may compete for the best positions. For this reason, social status can be an important determinant of positioning behaviour (Calf et al. 2002; Napper et al. 2013; Ost et al. 2007; see Fig. 6.5). There are many examples of dominant animals occupying central positions and displacing subordinates to the periphery of groups. For example, subadult coatis (*Nasua nasua*) are forced to occupy positions at the periphery of groups in the face of aggression from adults (Hirsch 2011). Similarly, younger, subordinate willow tits (*Parus montanus*) are excluded from the best feeding sites and forced to occupy more risky positions in the group (Ekman and Askenmo 1984; Ekman 1987). Despite these clear disadvantages, however, subordinates are more likely to survive the winter in groups containing dominants compared to groups where the dominants have been experimentally removed (Hogstad 1989). Planktivorous

Fig. 6.5 Mean dominance score of male (*solid bars*) and female (*open bars*) long-tailed tits (*Aegithalos caudatus*) in relation to their position in a roost (From Napper et al. (2013))



coral reef fish, such as fairy basslets (*Gramma loreto*), live in aggregations at the edge of reefs and feed on plankton. Dominant individuals occupy the most productive sites, forcing subordinates to the margins of the group where feeding opportunities are limited (Webster and Hixon 2000).

Dominant birds in foraging groups of barnacle geese (*Branta leucopsis*) obtain the most favourable foraging positions and so are able to maximise their intake. By contrast, subordinate birds are displaced from the best positions and suffer from the depletion of resources caused by higher-ranking individuals. In an attempt to counteract this, subordinates may adopt alternative foraging strategies, particularly adopting greater mobility in the search for food (Rowcliffe et al. 2004; Rands et al. 2006). Another alternative strategy for a subordinate animal is to attempt to seek out its own foraging patches rather than to compete at an existing patch. However, even when it manages to locate a foraging patch, the subordinate may be excluded from it after a short period of time or may suffer kleptoparasitism by more dominant group members; hence, subordinates may often act as producers in this respect (Beauchamp 2014; Webster and Hart 2006a).

In addition to monopolising the best relative positions in the group and the best foraging patches in the environment, dominants often occupy safer parts of the environment, forcing subordinates to occupy sites where the predation pressure is greater. In many bird species, dominant animals in foraging groups may be found closer to shelter, or in safer parts of vegetation, than subordinate members of the same group (Ekman and Askenmo 1984; Hogstad 1988; Koivula et al. 1994; Schneider 1984). Indeed, moving to riskier parts of the environment may be the price that subordinates have to pay in order to gather sufficient food (Halley 2001). These foraging sites are not the preferred option of the subordinates, as can be demonstrated by the tendency of these animals to switch to safer areas when dominants are removed (Ekman and Askenmo 1984; Desrochers 1989; Slotow and Rothstein 1995; Krams 1998). As well as being forced to forage in riskier places, subordinate animals may have to forage for longer and at times of day when risk is greater in order to satisfy their nutritional requirements. For many diurnal species, especially those that rely on vision to detect predators, dawn and dusk represent risky times to forage, because predators concentrate their hunting efforts at these times of day (Bosiger and McCormick 2014; Lahti et al. 1997). It seems likely that these constraints on the behaviour of subordinate animals translate to higher per capita predation risk, and certainly studies have reported that subordinates are disproportionately vulnerable to predators (Ekman 1986). However, dominance often covaries with a range of different characteristics, including age and size, which can make it difficult to determine the precise effect of subordination on risk. We return to the topic of dominance and its relationship to competitive ability in the following chapter.

6.5 Summary

To many laypersons, the term ‘sociality’ connotes collaboration and teamwork. For this reason, social animals are sometimes assumed to show higher levels of cooperation than other, less gregarious species. While this may be true in some species and in some contexts, individuals in most animal groups typically pursue their own selfish ends, competing to obtain a maximal share of resources while at the same time seeking to pay as low a cost as possible. This pursuit of individual objectives means that while sociality generally provides a net benefit to all, the distribution of the payoffs of social group membership is not equal. Many excellent studies have been published documenting these inequalities and relating these to dominance hierarchies and to positioning behaviour within groups. Often, however, these studies represent a snapshot of life within the group, whereas we know that the positions of animals in groups change dynamically. Even the social status of animals can alter, in some cases quite rapidly. To build on such studies, it would be extremely valuable to take a longitudinal approach in order to examine the benefits realised by individuals over time and the costs paid. Integrating behavioural studies with real-time physiological data would provide a fascinating insight to the motivational forces which drive the positioning behaviour of animals and would also yield greater understanding of the benefits and costs of different positions over time and across contexts, particularly in relation to foraging. In addition, studies may focus (often for good reason) on a single specific benefit, such as foraging reward, or a particular cost, such as predation risk. Yet to fully understand the behavioural strategies of social animals, we need to consider the fullest possible range of factors weighed by animals in making their decisions.

Group Size

7

7.1 Introduction

The naturalist John James Audubon famously gave an account of a migration of the now vanished passenger pigeon (*Ectopistes migratorius*). After attempting to count the passing flocks that together made up the vast procession, he abandoned this task as impractical and continued on his journey, noting that at the end of a full day's travelling the birds still continued to pass by and did so still for several more days thereafter (Audubon 1870). Breeding colonies consisting of hundreds of millions of pairs of these birds were reported during the 1800s, and it is estimated that the largest migrations contained billions of individuals (Schorger 1955). During the latter decades of the nineteenth century, as Americans in the eastern states bore witness to these huge flocks, those living further west were contending with periodic outbreaks of another multitudinous animal, the Rocky Mountain locust (*Melanoplus spretus*). One infamous swarm of 1875 was estimated to have covered half a million square kilometres and to have contained several trillion locusts (Piper 2007). Like the passenger pigeon, the Rocky Mountain locust was to be extinct shortly after the turn of the century. Today, juveniles of the extant – though declining (Atkinson et al. 2004) – Antarctic krill (*Euphausia superba*) in the Scotia Sea of the Southern Ocean form super swarms trillions strong that can be 30 m deep and extend over several km, sometimes containing hundreds of individuals per cubic metre. So large are these swarms that the majority of the total population can be contained within just a few such aggregations (Tarling et al. 2009).

Clearly these are extreme examples, atypically large aggregations that fall towards the farthest end of the range of group sizes seen in nature. While smaller groups are far more common, group size can be highly variable, even within populations, and it is not uncommon among some species to find groups whose sizes differ by two or more orders of magnitude (Sinclair 1977; Bonabeau et al. 1999). In this chapter, we ask what are the causes and consequences of group size variation. First, we will look for generalities in the distributions of group sizes seen in populations under natural conditions. Next, we examine the extent to which

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observed group sizes match theoretically predicted optima and look at the factors that might cause observed group sizes to deviate from these. We will then look at the different ways in which the animals themselves can influence group size. Finally, we consider how group size affects behaviour, including quantitative and qualitative differences in the behaviour of groups of different sizes, and ask how the behaviour of the individual and the group as a whole are affected by group size.

7.2 Group Size Distributions

The sizes of animal groups seen in nature are often determined by the environment, with ecological conditions playing a role in determining both upper and lower limits on group size. On the one hand, larger group sizes may be constrained by the availability of food, shelter or other resources. The sizes of breeding colonies of some seabirds, for example, appear to be limited by intraspecific competition for prey near to the colony (Furness and Birkhead 1984). At the other end of the scale, there may be a minimum group size for groups, beneath which group members are unable to defend territory, resist predators or maintain homeostatic function. In an illustration of the latter, larvae of the leaf notcher moth (*Pryeria sinica*) group together and spin a silk nest web in order to avoid desiccation. Tsubaki (1981) found that a minimum group size of more than 30 larvae was necessary for groups to survive, and that groups containing fewer than this tended not to become established successfully. Differences in food availability between open woodland, forest clearings and dense woodland have been suggested to be one factor that drives herd size differences seen in sika deer (*Cervus nippon*) living in these habitats (Borkowski and Furubayashi 1998). Environmental perturbation can also drive changes in group size. In toque macaques (*Macaca sinica*), usually stable groups can fragment into independent troops when placed under environmental stresses arising from cyclones or droughts (Dittus 1988). The environment may affect group sizes in other ways too, for example, by placing limits upon the frequency with which smaller units encounter each other, in turn affecting the rate at which they can coalesce into larger groups (Gerard et al. 2002).

As a general rule, very large groups tend to be rare, while small groups occur much more often. In other words, group size follows a power law distribution, albeit limited by the size of the population, such that a plot of group size against proportion of observations shows many groups containing a few individuals, before decaying into a long, rightward-progressing tail in which numerically larger groups occur with decreasing frequency. Such distributions of group size frequency have been described for a range of ungulates and fishes (Bonabeau and Dagorn 1995; Bonabeau et al. 1999; Niwa 2003). From a group-level perspective then, smaller groups tend to be more common; however, at any given time, most individuals within the population will tend to be contained within intermediately sized groups.

7.2.1 Group Sizes in Open and Structured Environments: Ecological Versus Emergent Explanations

A number of studies have noted that for species that range across different habitat types, group sizes tend to be larger in open habitats, such as grasslands, compared to more structurally complex areas, such as scrub or forest. Similar observations have made for related species that differ in their habitat use. While this has been noted particularly in free-ranging ungulates (Gerard and Loisel 1995; Gerard et al. 2002), similar findings have been reported in laboratory studies of shoaling fishes (Orpwood et al. 2008; Webster et al. 2013). Frequently, ecological explanations are invoked for these observations; group size is limited by food availability, which differs between habitat types, or cover reduces risk of detection by predators, favouring larger group sizes in the open, for example. Gerard and Loisel (1995) and Gerard et al. (2002) have argued that such adaptive, ecological explanations are not strictly necessary to account for this pattern however. They suggest that larger group sizes in open habitats may emerge from smaller groups being able to detect one another over greater distances, increasing the rate at which they fuse to form bigger units. It is possible that both mechanisms – ecological causes allied to the ease with which animals can detect and aggregate with one another – play a role in group size here, and further research is needed in order to determine the relative importance of each.

7.2.2 Individual Behaviour and Fission-Fusion Models of Group Formation

Theoretical approaches have made use of fission-fusion models to attempt to explain this power law distribution of group sizes (Bonabeau and Dagorn 1995; Bonabeau et al. 1999; Niwa 1998, 2003). These approaches typically make a number of assumptions, such as that animals are free to join or leave groups, that their propensity to do so is independent of the size of the group, that animals mix randomly and exhibit no preferences for associating with particular individuals or phenotypes and that the environment within which the groups move is either homogenous or that grouping behaviour is not affected by local environmental conditions. Krause and Ruxton (2002) noted that work on group choice by individual animals is at odds with some of these assumptions. They point out that in nature, groups are frequently assorted by phenotype, that individuals can have preferences for larger or smaller groups at certain times and that they sometimes preferentially associate with some group mates more than others. These points are supported by research carried out on the shoaling behaviour of several species of small fishes, a model system for the experimental study of grouping behaviour. Here it has variously been shown that fish assort by phenotype (Hoare et al. 2000a, b), that they form heterogeneous association networks (Croft et al. 2005), that they preferentially group with familiar individuals (Ward and Hart 2003) and in some species kin (Piyapong et al. 2011) and that shoaling decisions are strongly influenced by external cues (Hoare et al.

2004). Here then there is scope for integrating information about group joining bias from studies that consider grouping behaviour at the level of the individual, with modelling approaches that consider the processes leading to the emergence of different group sizes.

7.3 Are Group Sizes Optimal?

Given that animal group sizes are observed to vary between habitats, change in response to climatic perturbations and that groups are not composed of random subsets of the populations, but are in fact sorted by a range of different factors, we might ask whether group sizes are most appropriate for the local environment. Do they reflect the best possible balance between the costs and benefits of grouping for the individuals that comprise the group? In other words, should we expect observed group sizes to be optimal?

The simplest answer to this question is in most cases ‘no’, although there are exceptions: Baird and Dill (1996) showed that transient-form orcas (*Orcinus orca*) that were hunting seals typically did so in numbers that maximised their energy intake, for example, but in general there are convincing theoretical arguments for expecting group sizes to tend to exceed the predicted optimum (Sibly 1983). Before looking at why group sizes close to the predicted optimal size are not often seen, it is worth first considering what is meant by optimal and how this is determined.

As we saw in Chaps. 4, 5 and 6, animals can benefit from grouping with others in a number of ways, but they also pay costs. The optimum group size is the one that represents the best possible compromise between the advantages and disadvantages of grouping with others. Here, optimality is measured in fitness, specifically the expected fitness returns of the individuals that together comprise the group. In theory, a biologist could identify all of the benefits and all of the costs that accrue from being part of a group and determine their net effect upon fitness. This may even be possible for certain study systems under certain conditions. In practice of course, this can be very difficult to do, particularly in the field. Moreover, most studies of group size do not focus upon ultimate fitness, but instead quantify some proximate, functional outcome. The question of optimal group size then, is *optimal for what*? What aspect of the animals’ lives, if any, is optimised by being in a group of a particular size? This issue is highlighted by a series of studies on the sizes of prides of lions (*Panthera leo*) in the Serengeti. Caraco and Wolf (1975) noted both that although prey capture rate increased with increasing pride size, the per capita share of food decreased and that the number of lions taking part in hunts typically exceeded that which would result in the best balance between the likelihood of a successful hunt and the share of the kill. Packer et al. (1990) argued that group sizes might not be geared towards maximising prey intake, but that they instead might reflect the need to defend cubs or hunting territories. Deciding what to measure and in what context to approach the question of group size optimality is very important.

A further problem in determining what the optimal group size ought to be is that the costs and benefits to the individual of group membership can be highly dynamic, meaning that the predicted optimal group size can vary between locations and over time. Yet another consideration is that individuals are likely to differ from one another in a number of different ways, including in terms of their nutritional requirements, or ability to compete for resources, meaning that the optimal group size for some members can be suboptimal for others. Inequality in the benefits of grouping is an issue we return to below. Perhaps foremost among the reasons that optimal group sizes are predicted to be rarely seen, and indeed are often exceeded, is the expectation that individuals are self-interested and are likely to behave in ways that maximise their own fitness, even if doing so reduces the fitness of the other members of the group.

7.3.1 Larger than Optimal Group Sizes: The Sibly Model

Richard Sibly (1983) argued that self-interested behaviour can render group size unstable and cause observed group sizes to exceed the theoretically predicted optimum. This occurs because up until a certain group size is reached, it may be better for an individual to be in a larger than optimal group than for it to be alone, which in turn should lead newcomers to join groups even when doing so drives down mean group member fitness, so long as doing so benefits the joiner. Figure 7.1 presents a hypothetical illustration of Sibly's (1983) model. Imagine finches converging on a large meadow to feed from the seed heads of thistles. The thistles occur in many patchily distributed clumps, and as the finches arrive, they have the option of landing at clumps that other birds are already feeding at, joining them to form groups, or of landing at unoccupied thistle clumps and foraging alone in another part of the

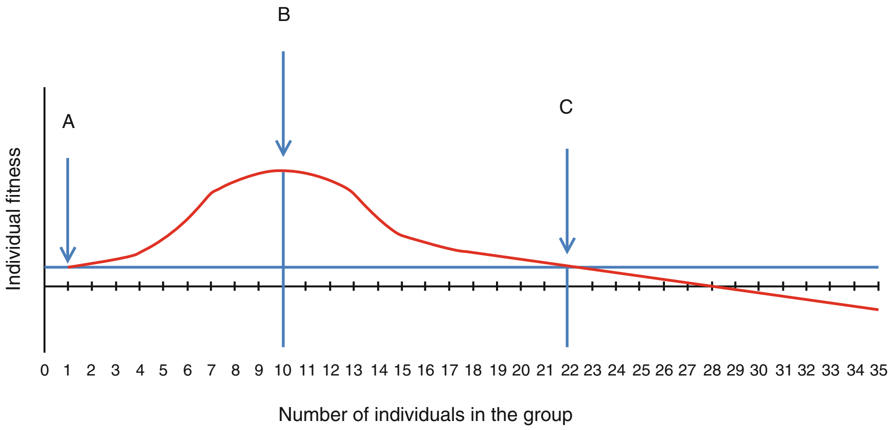

Fig. 7.1 The fitness payoffs of being in a group of a given size. [*A*] shows the fitness payoff of remaining alone, [*B*] the theoretically predicted optimum group size, which maximises mean fitness to group members and [*C*] shows the Sibly size (After Sibly (1983)). The Sibly size is the size at which a newly arrived individual would do as well by joining as it would if it remained alone. Note that the Sibly size [*C*] exceeds the optimal size [*B*] by some margin

meadow. Being alone or being in a group of a given size carries a particular fitness return. The fitness returns for different group sizes of our hypothetical finches are shown in Fig. 7.1. The expected fitness for a finch foraging alone is fairly low, since it is highly vulnerable to predation, so if a newly arriving finch is able to see another finch foraging, it will on average do better if it joins the forager than it will if it alights at an unoccupied clump of thistles. In fact this benefits both individuals – the individual fitness returns are higher for birds in a group of two than if each is alone. Two finches are more likely to spot approaching sparrowhawks than are loners, and because both are looking out, each can afford to invest a little more time in seeking out and extracting seeds, gaining more energy in the process. This effect continues as group size increases, such that three birds foraging together enjoy greater fitness than do pairs, and members of a group of four can expect on average to do better still. There is, however, an upper group size limit on this effect, the predicted optimal group size, and once this is exceeded, mean individual fitness begins to fall. For our finches in Fig. 7.1, the predicted optimal group size is ten. The thistle clumps can only support so many finches, and if too many are present, then the birds may interfere with each other's searching, reducing foraging efficiency, or engage in bouts of noisy squabbling over seeds which might draw the attention of predators more often than more amicable foraging behaviour. Given this then, from the perspective of the individuals already in the group, it is best to number exactly ten. But if an additional finch arrives at the meadow, what should it do? It has the option of joining the flock of ten or of foraging alone on a separate clump of thistles elsewhere. Although the fitness returns for individuals in a group of eleven are lower for those in a group of ten, they still greatly exceed that of a lone individual. It therefore pays the newly arrived finch to join the group of ten. Though the original group members' fitness is now reduced somewhat, the self-interested new arrival can expect to do far better than it would if it were by itself. This pattern can be expected to continue as further finches enter the meadow. As newly arrived birds cause the group size to swell, the fitness returns of those already in the group continue to fall, but so long as it remains better for a new bird to join the group than to go it alone, they should be expected to do so. Eventually, a point is reached where the group is so large that it is no longer the best strategy for an incoming finch to join the group. In the case of Fig. 7.1, an individual in a group numbering twenty-two has the same expected fitness as it would if it were alone. If another bird were to enter the flock, the fitness of its members would actually be lower than if they were to forage independently. When the twenty-third bird arrives in the meadow, it would do better to forage by itself than to join the group. This point is sometimes known as the Sibly size.

The fitness curve, the plotted relationship between group size and fitness, is likely to vary greatly depending upon the species concerned, and as a function of the environment and the various pressures to which the group is exposed. In simple terms, this will affect the predicted optimum group size – some environments will favour larger groups, whereas in others only small groups will prosper. Environmental conditions may shape the fitness curve in more subtle ways too. For example, for a shoal of fish foraging over a rocky lake bed, where predators may be less able to detect them and where they have lots of cover to hide among and evade capture, fitness may increase slowly as group sizes increase, while for the same fish foraging in open water where there is nowhere to hide, a steeper increase in fitness might be expected. In other cases, fitness may increase significantly only once a threshold group size has been reached. Such a scenario might apply to animals that group for homeostatic reasons. Animals may huddle in order to minimise exposed surface area so as to regulate heat or water loss, and a minimum number of individuals may be required to effectively achieve this.

Another biologically plausible scenario is one of diminishing returns. Once a few individuals have gathered together, the arrival of still more group members might increment individual fitness returns ever more slowly. This effect may occur where the main detriment to fitness is determined by risk of being eaten by a lone predator than can only tackle one group member at a time and which only feeds once during a hunting bout. Assuming that all group members are at equal risk, the rate of decline in per capita predation risk falls ever more slowly as group size grows, falling first to 50 %, then 33 %, then only 25 % and so on, as lone individuals become part of a pair, a trio and then a quartet, while competition for finite resources such as food or space goes up and up, further slowing the net fitness benefit of grouping.

Similarly, the rate of declining fitness once the optimal group size is surpassed may be expected to vary too. In our hypothetical finch example in Fig. 7.1, once the optimum group size is exceeded, the decline in fitness initially matches the increase in fitness seen as it was approached, such that the individual fitness for a group size one less than optimal was the same as that for a group containing one more than was optimal. Following this, the rate of decline in fitness returns slows, producing a tail, such that the group size at which fitness is lower than being alone is actually more than twice the optimum size. Of course the fitness curve need not be symmetrical around the optimum at all. Fitness may decline very slowly, decaying into a long tail that might permit observed group sizes to exceed predicted optima several times over, before it no longer pays to join the group. There may also be threshold effects, beyond which fitness declines precipitously. The latter may occur in swarms and schools of some krill and fish species, where large or dense groups can quickly deplete oxygen levels, a factor that influences the size, shape and density of their groups (e.g. Brierley and Cox 2010). In an extreme extension of this scenario, Giraldeau and Gillis (1985) posit a situation where the fitness of the group's members drops below that of a lone individual if the optimal size is exceeded by just one. Under such conditions, we would expect to frequently observe that group sizes that do not exceed the optimum.

7.3.2 Accounting for Competitive Differences Between Individuals: Skew Theory

Survival curves that plot individual fitness against group size make a number of assumptions, a major one being that the fitness payoffs of grouping are the same for all group members. Frequently, this will not be the case. An individual's position within the group can strongly affect its fitness (see Chap. 6). Those at the front of a travelling group may be more likely to detect or reach food sooner than those towards the centre or rear (Krause 1993b) and may therefore gain more energy. On the other hand, those at the front and those generally occupying more peripheral positions may be more likely to be attacked by predators (Hamilton 1971; Krause 1994). Oddity effects are important in mediating predation risk too – if an animal looks or behaves differently from the rest of its group, or from its near neighbours, then it may be more likely to be singled out by a hunting predator (Landeau and Terborgh 1986; Ioannou et al. 2012, see Chap. 4). Local differences in group density, the number and closeness of neighbouring group mates, can also bear upon an individual fitness, affecting things such as resource competition or their likelihood of being attacked (Ioannou et al. 2009). Animals in mobile groups, particularly those travelling through water or air, might also gain energetic benefits from their position relative to others in the group (Fish 2010).

Another source of variation between individuals in the fitness returns that they receive from grouping stems from differences in competitive ability and dominance. Competition among group members can be intense. The presence of individuals that are bigger, more experienced or otherwise better equipped to gain a greater share of a limited resource can result in variation between members in the fitness benefits of grouping. If the disparity in fitness between dominant and subordinate group members becomes too great, so that the expected fitness of the worst-off members becomes lower than if they were alone, then it may pay them to leave the group. This, in turn, may be detrimental to the fitness of the dominant individuals, who are now in a smaller group. Under these circumstances, the dominant individuals might be expected to reign in their command over the contested resources, allowing the subordinates to increase their share to the point that the fitness returns of their remaining with the group are equal to or better than those of leaving it. The theoretical framework developed by researchers seeking to quantify the dynamic conflict between dominant and subordinate group members over fitness determining resources is called skew theory (Vehrencamp 1983; Keller and Reeve 1994; Hamilton 2000).

Dominant individuals may enhance their own fitness at the expense of that of more subordinate group members. In the case of communally breeding species, where the capacity of the colony to successfully raise young is limited, dominants may suppress reproduction among subordinates, through infanticide or by evicting those that attempt to breed, for example. If a subordinate member can expect to do more poorly by itself than it can in the group and if the dominant member of the group is able to eject the subordinate if it engages in any behaviour that reduces the dominant's own fitness, then the dominant member can exert control. Under such circumstances, it is in the interest of the subordinate to modify its behaviour so as not to infringe upon the fitness of the dominant. If enough subordinates leave the group that the fitness of the remaining dominant members begins to fall, which may occur, for example, if a minimum group size is required for territory defence, effective hunting of large prey or for communal raising of young, then the subordinates now have some leverage, and it is the dominant individual that may do better by relinquishing some opportunities for reproduction to the subordinates so as to maintain the critical group size.

The predictions of Vehrencamp's (1983) original optimisation models are supported by data on the reproductive behaviour of a cuculid bird, the groove-billed ani (*Crotophaga sulcirostris*). In anis, where several pairs share and lay eggs in a communal nest, the eggs of early breeders are often ejected by other group members, such that the largest proportion of the eggs remaining in the clutch tend to belong to the dominant, last breeding pair. While subordinate females can expect to raise comparatively few young when breeding as members of such a group, their lifespan is generally much shorter if they attempt to breed alone. Their lifetime reproductive output then, which takes into account both the number of chicks fledged per year and the total number of years that they survive to reproduce in, actually tends be greater if they breed as a subordinate group member, even allowing for the high risk of egg ejection by their more dominant group mates (Vehrencamp 1978, 1983). These data illustrate why subordinate members of groups often tolerate what on the face of it appears to be a very poor deal and demonstrate the importance of considering lifetime reproductive success when thinking about the fitness payoffs of behavioural strategies.

Reproductive skew theory has more recently been tested using long-term data sets on the group composition and individual reproductive behaviour of breeding groups of mongooses (*Mungos mungo*) (Cant et al. 2010). Such breeding groups typically contain several dominant females as well as a number of subordinates. The dominant females generally produce the most young, but subordinates may breed too. If the number of young produced becomes too great then the mortality rate of the pups, including those of the dominant females, can rise. When this occurs, the dominant females may respond by driving breeding subordinate females out of the group. During a breeding bout, all females in breeding groups become sexually receptive at the same time, and interestingly, despite the threat of eviction, most of the subordinate females mate and conceive during this period too. Some of the subordinates, when evicted, abort their young and are allowed to re-enter the group by the dominant females. This strategy permits a degree of flexibility on the part of the subordinates, allowing them to seize the opportunity to breed when it is available or abort so as to avoid permanent eviction when it is not, instead of paying the fitness cost of missing breeding opportunities by exercising pre-emptive restraint.

Vehrencamp's (1983) original optimisation model focussed upon the conflicts over fitness returns among differently ranked members of communal breeders. In principle, skew theory models can be applied to the fitness payoffs associated with other grouping interactions too, such as social foraging. Hamilton (2000) did just this, using skew theory to make predictions about group size among foragers, under conditions in which dominant individuals were able to control access to food resources. Here, if it benefits the dominant individual to be joined by other, subordinate foragers, it allocates them a share of the food such that their fitness payoff from being in the group is equal to that that they would receive if they were foraging alone. Food withholding behaviour by the dominant individual can be used to predict the stable size of the group, assuming that the foraging success of the group increases with group size, but at an ever diminishing rate. Under such conditions, the model predicts a stable group size that exceeds the optimal group size that might be expected if resources were shared equally among members, but smaller than the large group sizes predicted by Sibly's (1983) model, where individuals remain within the group so long as they gain marginally higher fitness returns than they would if they were alone.

7.3.3 Accounting for Relatedness

The Sibly (1983) model and the derived hypothetical fitness curves make no assumptions about the degree of relatedness between the group members and prospective joiners. A number of researchers have noted that relatedness and resulting inclusive fitness effects may be expected to have a substantial effect upon the shape of the fitness curve and the maximum expected group sizes. These effects can be modelled and used to generate predictions about group joining decisions under different conditions (Giraldeau and Caraco 1993, 2000; Higashi and Yamamura 1993). Giraldeau and Caraco (1993) point out that when thinking about how inclusive fitness might affect group size, we also need to account for whether the group is open in nature or whether access is restricted (indeed this is also true for groups in general). In open groups, incoming members are free to join the group and the existing group members are unable to stop them. In contrast, in restricted entry groups, the existing group members are able to repel would-be joiners, stopping them from entering the group.

Let us first consider a group where individuals are free to join. If the group is currently below its theoretically predicted optimal size, then incoming individuals do best to join the group, and the existing group members enjoy greater fitness too. Under these conditions, an incoming individual faced with the choice of joining either of two equally sized groups consisting of either relatives or non-relatives would be expected to join the group to whose members it is related. Once the optimal group size is reached, mean fitness for those already in the group will fall if any more joiners arrive. Here the new arrival is expected to join the non-related group, since it would pay the cost of reduced inclusive fitness if it joined its relatives.

What about a newly arrived individual faced with only one group that has already reached or exceeded its optimal size? It has the choice of joining it or remaining alone. Assuming that newly arriving individuals are unrelated to those already in the group, it is in their interest to continue to join the group until the mean fitness is equal to or less than that of a lone individual, as per Sibly's (1983) original model. If the incoming individuals are related to those already in the group however, then by joining a group that has already reached its theoretically predicted optimal size, they lower the mean fitness of those already in the group, which in turn reduces their own, indirect fitness. The extent of this indirect fitness cost will be affected by their mean relatedness to the other members of the group, the number of relatives affected and the size of the fall in fitness caused by their arrival. Weighing against this cost is the increase in direct fitness that the joiner receives, compared to if it had opted to remain alone. All else being equal, increasing relatedness between the existing group member and the would-be joiner is expected to result in lower stable group sizes, compared to scenarios where joiner is unrelated to those already in the group.

Consider now restricted entry groups. When the incoming individual is unrelated to those already in the group, and the group members are able to recognise this and prevent it from joining, we would expect to see maximum group sizes that correspond to the theoretically predicted optimum. Group members should allow the group to swell to the point where their fitness is maximised and then reject further members. On the other hand, where newly arrived individuals are related to those within the group, they should be permitted to join, so long as the direct fitness costs to the original group members are offset by the inclusive, indirect fitness that they gain from admitting relatives.

Accounting both for relatedness and for whether entry to the group is controlled by the joiners or the current members, the largest group sizes, or more specifically the group sizes where mean fitness extends furthest beyond the theoretically predicted optimum, are expected for scenarios where unrelated individuals are free to join existing groups. The group sizes that deviate least from the theoretically predicted optimum ought to occur in groups where the current members can exclude new members and potential joiners are unrelated to them (Giraldeau and Caraco 1993; see Chap. 1).

The predictions made by the models of Giraldeau and Caraco (1993, 2000) are experimentally tractable, though comparatively little empirical research has been carried out here. We speculate that group joining rules based upon relatedness might be more common when incoming individuals are faced with relatively stable groups, such as kin-assorted communal breeders or territory holders, where group composition changes relatively slowly. In more volatile groups, such as the large, free-entry flocks and shoals typical of many birds or fishes, where groups frequently meet and exchange members and where mixtures of close and distant relatives are found together, accurately assessing relatedness or tracking changes in the numbers of relatives within the group might be impossible.

7.4 Proactive and Reactive Grouping Decisions: How Can Animals Modify Group Size?

Skew theory deals with the ways in which animals can influence group size; dominant members of communally breeding societies can curtail reproduction among subordinates or eject them completely from the group. Alternatively, when it suits them, dominants persuade subordinates to remain within the group by making additional resources available to them. In addition to this, social animals can directly influence group size proactively by actively recruiting new members, by evicting others and by generally exercising control over their own or leaving decisions. Such mechanisms tend to be observed primarily in restricted entry groups. In other social species, particularly those living in free entry groups, group size is an emergent and dynamic outcome of the reactions of individuals to context and to proximate conditions. We consider these two alternatives separately.

7.4.1 Proactive Grouping Decisions

7.4.1.1 Recruiting Members

There are situations when it might pay group members to be joined by others, such as to reduce their risk of being captured by a predator, to increase their foraging efficiency or to maximise homeostatic benefits, for example. Under these circumstances, they may actively solicit others to join the group by producing a signal, such as a call or chemical message, a process known as recruitment. Here, we define a signal as a cue that alters a receiver's behaviour that evolved for that effect and which is effective because the receiver's response has also evolved (Smith and Harper et al. 2003). There is a great deal of experimental and observational evidence that various species of animals do indeed perform behaviours or produce signals that might function to enable others to locate them or induce them to join them. Determining whether a cue produced by a group member actually functions as a recruitment signal, rather than being merely a passively produced by-product of its behaviour which the joiner can detect and capitalise upon, is not always straightforward, however. This distinction is important because there are circumstances where joining the group might benefit the joiner but be detrimental to the fitness of those already in the group, conditions under which the effect of signalling to others to join would be costly to the signaller. Herein lies a challenge for researchers: how to distinguish between true cases of active recruitment and cases of inadvertent social information use by joiners. Krause and Ruxton (2002) produced a useful checklist for assessing whether a cue most likely does function as a signal by which further group members are actively recruited or whether it is an inadvertent by-product exploited by observant joiners. They suggest that in order to qualify as a likely case of recruitment signalling, the following criteria must be fulfilled:

1. The putative signal must not be obligate. In other words, the signaller should be able to engage in whatever behaviour it is performing without necessarily producing the signal. For example, for a bird feeding on grains on the ground, head-bobbing as it stoops to feed is a cue which might convey information to others that food is present but is also an obligatory behaviour – the bird cannot pick up the seeds without bobbing its head. In fact head-bobbing is used as a cue by scrounging spice finches (*Lonchura punctulata*) to locate others who are feeding (Coolen et al. 2001). In contrast, if the bird produces head-bobbing gestures that are not associated with attempting to pick food up, or if it produced some other signal such as a specific call, behaviours are not functionally necessary for feeding, the argument that joiners are responding to inadvertently produced by-product of feeding behaviour would be weakened.

2. The signal is associated with the resource to which the signaller is attempting to recruit the joiner to. If the hypothesised function of the signal is to attract others towards a patch of food, then we would expect that the signal is only produced by foragers that have found food and not at other times or in other contexts.
3. Over the longer term, the sender should receive a fitness benefit from producing the signal. A strategy that lowers the fitness of the individual using it is not evolutionarily stable and is not expected to persist within a population. A researcher seeking to determine whether active recruitment is occurring may therefore aim to determine whether behaviours that attract joiners increase, decrease or have no effect upon the putative recruiter's fitness. Ultimate measures of fitness are the lifetime reproductive success of the individuals performing the behaviour and indeed the fitness of their offspring and/or other kin. Data on these might be obtainable for well-studied populations or for species amenable to study in the laboratory. In other cases, where collecting data on lifetime reproductive success is not feasible, proximate measures of factors known or thought likely to increase fitness might instead be quantified and used to build a case for or against active recruitment as the likely mechanism behind the accretion of joiners.

7.4.1.2 Recruiting Among Related Individuals

There is good evidence for active recruitment among related individuals. Here, the signaller gains an inclusive fitness payoff by recruiting kin to its group to exploit resources that it has found, in addition to any direct benefits that receives itself from being in a larger group. Even if the recruiter pays a direct personal cost in being joined, if the inclusive fitness payoffs exceed this direct cost, recruitment is expected to be favoured by selection. In the pied babbler (*Turdoides bicolor*), fledged juveniles remain close to their parents and continue to receive care from them even after they have ceased to require direct provisioning. In providing this extended support, both the breeding pair who produced the juveniles and the alloparenting nest helpers produce a special recruitment call which is used to summon the fledglings to patches of food. This behaviour likely benefits the juveniles while they gain experience of foraging for themselves, providing a bridge between parental care and full independence (Radford and Ridley 2006, see Fig. 7.2). Recruitment to food has also been documented among members of a eusocial mammal species, the naked mole rat (*Heterocephalus glaber*). Here, workers produce odour trails, recruiting their closely related colony mates to tunnels in which they have found food (Judd and Sherman 1996). Recruitment of relatives to resources is perhaps best known from and most specialised in the eusocial insects. Honeybee (*Apis mellifera*) foragers or scouts that have located resources such as nectar- or water-rich flower patches or potential new nest sites perform the famous waggle dance when they return to the nest. This encodes information about the direction and distance to the resource (von Frisch 1967; Riley et al. 2005; Seeley 2009) as well as assessments of its quality and associated risk (Seeley et al. 2000; Abbott and Dukas 2009). Many species of ants

Fig. 7.2 Pied babblers produce a special 'purr' call which is used to attract independently feeding fledglings to food patches. This call is rarely produced when only adults or dependent young are present or when the breeding pair are building or sitting on the nest. It is thought to function as a means of supplementing inexperienced young after direct provisioning has ceased (From Radford and Ridley (2006))

lay pheromone trails to recruit nest mates towards resources (Hölldobler and Wilson 1990; Jackson and Ratnieks 2006).

7.4.1.3 Recruiting Among Unrelated Individuals

What of recruitment to groups where the group members may be only distantly related to one another, and where there is no obvious inclusive fitness benefit to the recruiting individuals? Here, active recruitment is expected so long as the fitness benefits to the recruiter outweigh the costs of being joined, as discussed above. A number of cases have been documented in which putative recruiters produce signals that attract others and that are seemingly only produced in association with the discovery of a resource or when the recruiter is attempting to leave one area and travel to another. In these examples, a fitness benefit to the recruiter has not been demonstrated, but seems plausible. Colonially breeding black-billed gulls (*Chroicocephalus bulleri*) produce a contact call as they leave the colony to forage that is thought to function as a recruitment call to other foragers. Initiators are more likely to make these calls than followers, and initiators that call are more likely to be followed than those that do not. Playback experiments have been used to show that this call is attractive to other gulls. It is suggested that gulls gain social foraging benefits when searching for food with others (Evans 1982). Carolina chickadees (*Poecile carolinensis*) vary the structure of their alarm calls in different contexts and produce characteristic calls that may function to recruit others to newly discovered patches of food (Freeberg and Lucas 2002; Mahurin and Freeberg

2009). The first bird to locate a food patch produces this distinct call more frequently before the next bird arrives to join it than it does immediately after it has been joined. Playback experiments of calls containing more or fewer D notes, the component of the song thought to be involved in recruiting other flock members, found that birds arrived at nearby feeding stations soonest when songs with more D notes were played (Mahurin and Freeberg 2009). Green woodhoopoes (*Phoeniculus purpureus*) call to their flock mates to follow them when they move into new areas of habitat. Birds that call are more likely to be followed than birds that do not. Moreover, birds that call but which are not followed have been observed to fly back to the group and repeat their calls, as if trying again to recruit followers. It is though that recruiting others may benefit the recruiter both by reducing its own risk of predation and by providing support if aggressive neighbouring groups are encountered (Radford 2004). Interestingly, the benefits of grouping do not apply equally to all group members in green woodhoopoes, and subordinate birds that might be outcompeted at food sites sometimes do not attempt to recruit when they leave the group (Radford and du Plessis 2003; Radford 2004).

7.4.1.4 Increasing Group Size Through Adoption and Abduction

In some instances, animals may increase group sizes by adopting or even abducting individuals from neighbouring groups. This has been well studied in the several genera of slave-making ants, whose workers raid the nests of other species, returning to their own colonies with larvae, and in some species adult workers. Slave-making behaviour is also known as dulosis. Abducted slaves assume worker roles, tending the brood and feeding workers in the slave-maker colonies. Typically, slave-makers specialise upon a single, often closely related host species. In some species, slave-making is obligate and in others it is facultative. This way of life appears to have evolved multiple times, possibly as a by-product of brood predation. D'Ettorre and Heinze (2001) provide a fascinating review of the evolution of slave-making.

Cases where individuals, here conspecifics, have been integrated into groups from neighbouring territories have been documented in the convict cichlid (*Amatitlania nigrofasciata*) (Wisenden and Keenleyside 1992; Lee-Jenkins et al. 2015). Here it is not clear whether the incomers are forcibly captured or prevented from leaving or whether they are passively adopted. In one study of the brood composition of convict cichlid breeding pairs, Wisenden and Keenleyside (1992) reported that almost one third of broods contained young from neighbouring territories. Parents typically only accepted foreign fry that were smaller than their own, rejecting or eating larger ones. Smaller individuals are less likely to outcompete the parent's fry and were shown to be more likely to be taken by predators. Fry adoption may therefore benefit the parents and their offspring's fitness through reduction of predation risk, with size selectivity by the parents mitigating against the costs of increased competition.

Apparent kidnapping behaviour has also been observed in communally breeding white-winged choughs (*Corcorax melanorhamphos*), where recently fledged young were seen to be switched between groups during aggressive territorial disputes (Heinsohn 1991), and in mongooses (*Mungos mungo*), where young are taken from the burrows of neighbouring groups during territorial disputes (Müller and Bell 2009). Such behaviours may function to augment the kidnapping group under conditions where a group's success is linked to its size (Kokko et al. 2001).

7.4.1.5 Eviction and Restricting Entry

When group sizes reach or exceed the point where the fitness of the members of the group begins to fall, group members may begin to evict current group mates, exclude potential joiners or they may themselves leave the group.

Control by Dominant Group Members

As we have already seen when considering reproductive skew, dominant female mongooses can limit group size by evicting subordinate breeders whose offspring might limit the survival of the dominant female's own young (Cant et al. 2010). Eviction and exclusion also occurs in groups of clownfish (*Amphiprion percula*). Clownfish occupy anemones, which serve as breeding grounds and refuges. These groups consist minimally of a breeding pair, but may also contain a number of subordinate helpers. The total size of the group is positively correlated with the size of the anemone. If the group grows too large, the breeding pair may suffer fitness costs. Buston (2003) reported that in anemones that were close to saturation, breeding pairs reduced or limited group size both by evicting some of the current subordinate members and by preventing others from joining the group.

Interactions Within Parent-Offspring Groups

Parents may evict young once they reach a certain stage of development, in order to make way for new offspring. This may play out as a form of the classic parent-offspring conflict (Trivers 1974). Here, selection favours behaviour by the offspring that is geared towards maximising its own fitness, by prolonging parental care and provisioning for as long as possible. From the parents' perspective, it is better to cease caring for their offspring as soon as they are able to function independently, in order to invest in the production of new young. Parents may compel their young to leave by aggressively driving them away, or by others means, such as reducing or ceasing food provisioning. For example, in California gulls (*Larus californicus*), parents withhold food from their young for longer as the young became older. Younger parents withheld food for the longest periods, consistent with their having greater expected reproductive potential compared to older parents (Pugesek 1990). In Montagu's harriers (*Circus pygargus*), parents begin to withhold food from their young as soon as they are able to hunt for themselves, although in years where food is abundant, the young are able to prolong parental care to an extent by chasing and begging or stealing food from their parents (Arroyo et al. 2002).

Another manifestation of the parent-offspring conflict as it relates to group size is siblicide. This occurs when individuals, usually dependent young, are killed or ejected from the group (with fatal consequences) by full or partial sibling nest mates. Selection on the parents favours the production of as many young as are likely to survive to independence, and sometimes more than this, since many birds produce more young than they might be expected to successfully rear, as insurance against offspring mortality, or in order to capitalise on unusually productive environmental conditions (Mock et al. 1990). From the perspective of self-interested offspring however, siblings are competitors for limited resources. A consequence of such competition is siblicide, usually carried out by older, larger or otherwise more dominant individuals against weaker rivals. Siblicide is well studied in a number of bird species (Mock and Parker 1998) as well as in some mammals, including spotted hyenas (*Crocuta crocuta*) where twin cubs that kill their sibling grow faster than those in pairs of twins where no siblicide occurs, faring almost as well as singleton cubs (Hofer and East 2008).

Siblicide may also take the form of cannibalism, which not only reduces competition but also provides nutrition. Nymphs of the European earwig (*Forficula auricularia*) kill and consume nest mates. What is more, they have been demonstrated to be able to differentiate between siblings and unrelated nest mates, killing and eating the latter sooner and more frequently. Siblicide may benefit direct fitness, but incurs inclusive fitness costs, indicating a role of kin selection in the evolution of siblicidal behaviour (Dobler and Kölliker 2010).

7.4.1.6 Other Ways of Controlling Group Size: Plasticity in Recruitment and Tactical Deception

More subtle ways in which group members may prevent others from joining them include avoiding drawing attention to themselves or to the resources to which they have access and by actively deceiving would-be joiners about the apparent profitability of entering the group. The first of these is seen among animals that recruit, or which perform behaviours that are consistent with recruitment. Spider monkeys (*Ateles geoffroyi*) foraging for fruit-bearing trees perform calls that are attractive to others. Subgroups containing dominant members call more frequently than do groups that only contain subordinates. This may be because dominant monkeys are able to monopolise the fruit growing on the tree, and so bear limited food competition costs, while gaining the antipredator and benefits of foraging in a larger group, while the subordinates face more severe competition for food. Food competition may also be the reason subgroups occupying smaller trees call less frequently than those in bigger trees, with more available food (Chapman and Lefebvre 1990). For similar reasons, in groups of green woodhoopoes, subordinate individuals are less likely to perform recruitment calls as they move in to new areas of habitat than are dominants. This may enable them to forage without competition from competitively superior flock mates (Radford and du Plessis 2003; Radford 2004).

Group members might also perform behaviours that deceive would-be joiners about the benefits of joining the group. There is evidence that signalling animals are sensitive to eavesdroppers, who might intercept their signals and join them, leading to competition. Within shoals of Atlantic mollies (*Poecilia mexicana*), males court females, directing more courtship effort towards larger females than to smaller ones. This is presumably adaptive, since larger females are on average more fecund. When rival males are nearby however, the signalling males switch to courting smaller and initially unpreferred females. This has been interpreted as a form of tactical deception, a tactic by which the signalling male can deflect rival attention

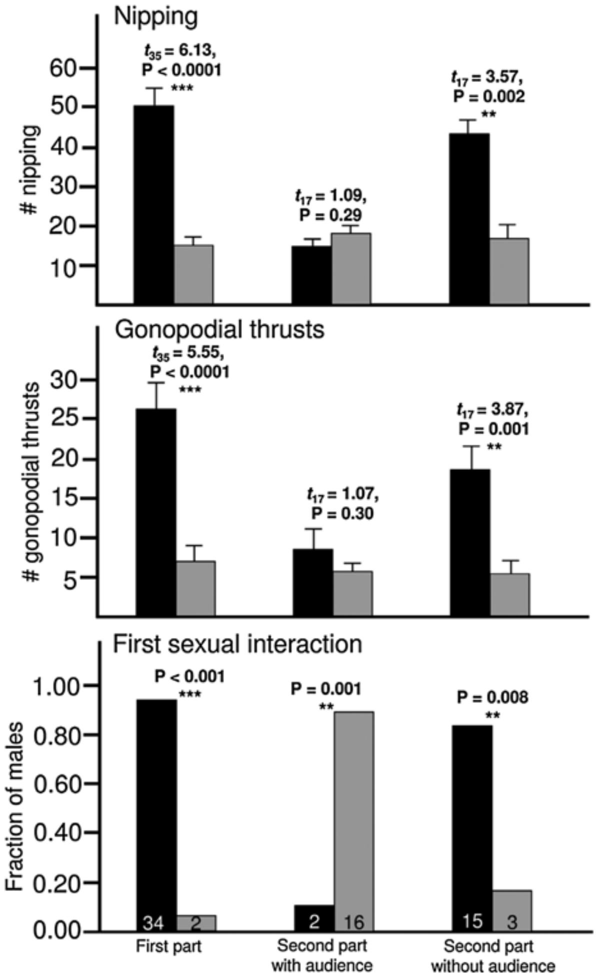

Fig. 7.3 Courtship behaviour of male mollies to large (*black bar*s) and small females (*grey bars*). In the first part of the experiment, when tested in the absence of a rival male, the test subject males directed more courtship nips, gonopodial thrusts and first sexual interactions towards the larger female. In the second part of the trial, half the test subject males were exposed to an audience consisting of a rival male. The test subjects ceased directing more nips and gonopodial thrusts towards the larger female and were more likely to attempt a first sexual interaction with the smaller one. The half of the males that were not exposed to an audience maintained their initial preference for the larger female (From Plath et al. (2008))

towards smaller females and minimising competition for the larger ones (Plath et al. 2008, 2010, Fig. 7.3). Mourning cuttlefish (*Sepia plangon*) are able to rapidly change colour and use this ability in a variety of contexts, including courtship. They are able to modulate their colouration with such precision that males can display courtship colouration to females on one side of their body while simultaneously displaying patterning that is not associated with courtship towards rival males located on their opposite flank. As with the redirected courtship behaviour seen in the mollies, this may function to deceive rival males and prevent them from joining and competing with the signaller (Brown et al. 2012). Both of these examples occur within the context of courtship and deal with male-male competition for females. It would be interesting to determine whether similar deception occurs within other functional contexts, such as foraging.

7.4.2 Reactive Grouping Decisions

7.4.2.1 Context-Dependent Grouping

One obvious way in which animals can maximise the benefits of grouping is by coming together only when it benefits them to, going their separate ways at other times. Such context-dependent grouping can occur at regular intervals, coinciding with daily or seasonal occurrences, or it can be employed reactively, in response to changes in the environment. Animals that group together to forage or migrate may, during the breeding season, disband into pairs or individuals that establish territories and actively repel conspecifics. Such seasonal shifts in grouping behaviour have been well studied in some passerine birds (e.g. Morse 1978). The opposite pattern can occur too, with animals that are largely nonsocial when not breeding coming together on a seasonal basis to reproduce, for example, as is seen in the colonially breeding grey-headed albatross (*Thalassarche chrysostoma*) (Croxall et al. 2005). Starlings (*Sturnus vulgaris*) provide an example of a likely adaptive diurnal shift in grouping behaviour. During daylight hours, they forage in smaller flocks, but at dusk, before settling to roost, they aggregate into far larger groups. This is thought to be an antipredator behaviour, and larger, denser flocks are seen at roosts where predation pressure is greater (Carere et al. 2009).

Hoare et al. (2004) provide a classic experimental investigation of reactive, context-dependent group size. They studied the grouping behaviour of multiple captive shoals of banded killifish (*Fundulus diaphanus*). If animals flexibly adjust their grouping behaviour in an adaptive way, they might be expected to form larger, denser groups when under risk of predation and smaller, more dispersed groups when feeding, so as to minimise the costs of competing with neighbours. This is what was seen in the killifish. In a treatment where they were exposed to conspecific skin extract, a cue associated with predation that is released from fish that have been injured by predators, the killifish formed larger, more tightly packed groups than they did when exposed to a control condition where only water was added to their pool. In another treatment, where they were exposed to chemical cues from food, they dispersed into smaller, more widely spaced groups than they did in the control condition. Finally, where they were exposed to both food and predation cues simultaneously, they formed groups of intermediate size (Fig. 7.4).

These examples look at how cues from the external environment can affect group-level responses in aggregating behaviour. Individual animals can vary in their sociability both in response to their own state and in response to the attributes of their would-be group mates too. This can result in subtle selectivity by individuals in when and with whom they group, with evidence again coming from laboratory experiments of fish shoaling behaviour. Krause et al. (1999) showed that hungry zebrafish (*Danio rerio*) preferred to join shoals of well-fed fish rather than groups whose members are also hungry. Doing so might allow them to gain a greater share of food than they would if shoaling with food-deprived group mates, who might be expected to compete more vigorously. European minnows (*Phoxinus phoxinus*) are able to recognise and prefer to shoal with poorer foragers (Metcalfe and Thomson

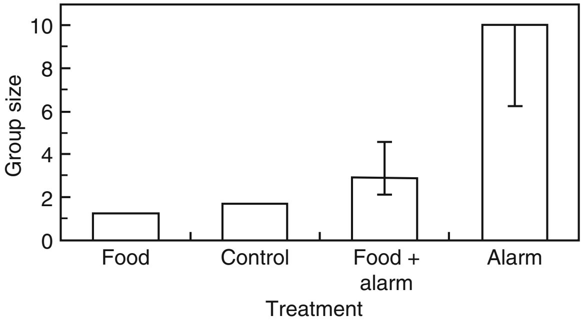

Fig. 7.4 Killifish disperse when exposed to food cues and form larger groups when exposed to alarm cues, a reliable indicator or predation risk. Group sizes are intermediate when exposed to both cues together and to well water (control) (From Hoare et al. (2004))

1995). Presumably, this gives them a competitive advantage while allowing them to retain other benefits of grouping.

7.4.2.2 Leaving the Group

When the benefits of grouping are not shared equally by all members, it might pay those who are doing badly to leave the group and join or search for another one. It has been observed that individuals of various species frequently move between groups when they meet, that groups often split and that when groups merge and split they sometimes exchange individuals (Croft et al. 2003). It is rarely clear however whether the individuals that move between groups are the ones who were doing most poorly in their old group or whether they gain any benefit from switching groups or leaving to go it alone. In fact, the mechanisms that underlie group departure decisions are not well studied, and this is an area that has received more attention from theoretical biologists than from empiricists. The consequences for group size of individuals leaving one group and joining another have been considered within the framework of the Sibly (1983) group size model, discussed above, while more recent models have attempted to elucidate the rules by which might spur an animal to leave one group for another.

7.4.2.3 Group Switching and the Sibly Model

Sibly's (1983) model, introduced in Sect. 7.3, can also be used to illustrate why individuals might be expected to move between neighbouring groups when they encounter one another and for understanding how such migrations might precipitate further movements in response. Consider again the example of finches foraging for thistle seeds in Fig. 7.1. This time there are 16 finches in the flock. Bear in mind that the theoretically predicted optimum group size is 10, so the finches could do better by splitting into smaller groups. We would not expect single birds to leave, since the fitness of being alone is much lower than being in the larger group. But if by some mechanism the flock were able to divide itself into two equally sized groups of 8, the mean fitness of all members would increase, since the fitness for being in a group of 8 exceeds that of being in a group of 16. This is not the end of the story however; 8 is better than 16 but is poorer than the predicted optimum size of 10. So now we might expect birds to leave one group of 8 and rejoin the other, forming a 9 and then a 10. This gives one group of optimum size and one suboptimally sized group of 6. Now, a bird in the group of 6 would do better if it left that group and joined the bigger one too, even though mean individual fitness now begins to fall again for the larger flock. This is true also for the next bird in the smaller group, and so on, until all of the members of the dwindling smaller flock have joined the larger one, and we are back at the starting point again, with one flock of 16 birds. Conceivably, such groups may split again, and group size might not be fixed but instead be dynamic, as individuals continuously move between groups in cycles of fission and fusion (Chap. 1). On the other hand, if the costs of moving are great enough, then group size might stabilise at some level. There is scope here for further research.

This invocation of Sibly's (1983) model is useful here both for understanding why group composition might be dynamic and group switching frequent and also for reemphasising how self-interested behaviour can maintain group sizes beyond theoretically predicted optima, as discussed in Sect. 7.3. Note that while we consider only two flocks of birds here, the same outcome, final group sizes that exceed the predicted optimum size, is also true for situations where many groups are exchanging individuals (Krause and Ruxton 2002).

7.4.2.4 Departure Rules

In some respects, the distribution of individuals between groups may be analogous to the way individuals distribute themselves between patches of resources, a concept known as the ideal free distribution (Fretwell 1972). Under the ideal free distribution, animals are at liberty to move back and forth between each of two or more patches. The profitability of each patch depends on a combination of both the amount and quality of the resource it contains and the number of others that are also present at the patch. Over time, the number of individuals at each patch is predicted to reflect its quality, such that the rate of resource uptake by each animal is the same at both. This might occur through the animals dividing themselves accordingly between patches and then remaining there, such that in a scenario with two patches, if one patch has twice as much of a resource, it ought to attract twice as many foragers. Alternatively, this could occur if all foragers constantly travel back and forth between the two patches, but spend twice as long in each foraging bout in the patch that has twice as much of the resource (Davies et al. 2012). Foragers should tailor the amount of effort they invest into exploiting a given patch according to some expectation of its yield (this is the 'ideal' in ideal free distribution, the assumption that foragers have knowledge of the relative quality of each patch). This expectation might take the form of a threshold resource intake level, below which the forager quits the patch for another, or a maximum search-to-discovery time limit, for example. In principle, such rules might determine not only patch residence but also group membership – an individual might switch groups upon exceeding some threshold level of cost, such as a minimum level of food intake, condition loss or reproductive output. This idea has been formalised by Beauchamp and Fernández-Juricic (2005). In their model, they assumed that foragers were able to learn about the distribution of food throughout the range of the population. In their simulations, foragers were allowed to leave the group if their foraging returns fell below that expected for the habitat as a whole. This allowed foragers to avoid under- and overcrowded areas, leading to group sizes that were close to the theoretically predicted optimum.

7.5 How Does Group Size Affect Behaviour?

Do groups of different sizes behave differently? And is the behaviour of individual group members dependent upon the size of the group that they are in? Social facilitation is a process whereby the presence of others can cause individuals to behave differently from how they otherwise might if they were alone. Facilitation may operate by a number of mechanisms, either alone or in concert. Animals may change their behaviour when in groups because the costs of remaining vigilant for predators are shared among many individuals, allowing them to engage in risky behaviours such as exploring further from cover or behaviours that are mutually exclusive from scanning for predators, such as feeding or courting. Competition may force them to change the extent to which they engage in certain behaviours too. An individual might be compelled to search for food for longer or in areas that it might otherwise avoid in order to maintain a minimum level of energy intake in the face of competition from others (Chap. 4). Quantifying the relative importance of these and other effects upon individual group member behaviour can be challenging (Beauchamp and Livoreil 1997; Grand and Dill 1999). Moreover, facilitation effects can interact with other aspects of behaviour, such as familiarity with the environment. In the mosquitofish (*Gambusia holbrooki*), activity levels were socially facilitated in novel environments, with larger groups being more active, but when the fish were familiar with their surroundings, there was no effect of group size upon activity levels (Ward 2012). This indicates that greater locomotory activity is not a consistent, group size-related pattern, but instead appears to vary with the amount of information that individuals hold about their environment. Novel environments may be perceived as risky, potentially because they may contain hidden dangers and because individuals have little or no information about the whereabouts of refugia.

Beauchamp and Livoreil (1997) found that in flocks of spice finches (*Lonchura punctulata*), vigilance levels initially decreased as group size increased, but once the group size reached a certain point, vigilance increased again. Seed handling time and search speed also fell as group size grew. They suggest that increasing levels of competition in larger groups could drive decreased vigilance, rather than enhanced foraging rates resulting from decreased investment in antipredator behaviours. A meta-analysis by Beauchamp (2008) of studies looking at the relationship between group size and vigilance found evidence of an overall trend for decreasing investment in vigilance, scanning and similar behaviours as group size increased, but noted that a substantial amount of the variation of these behaviours was unaccounted for.

Facilitation can affect behaviours other than exploration and vigilance of course. Palestis and Burger (1998) described social facilitation in the preening behaviour of common terns (*Sterna hirundo*), arguing that the role of facilitation in determining

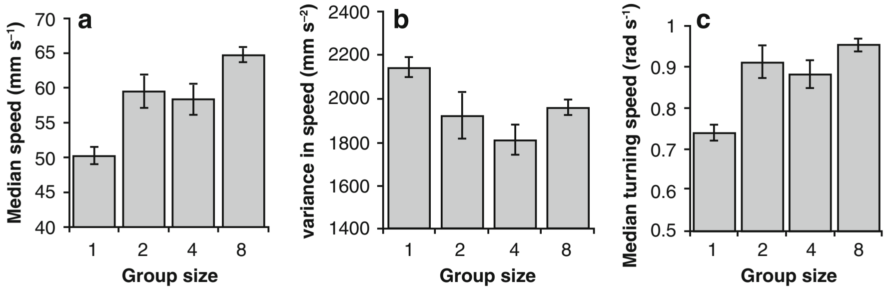

Fig. 7.5 Median (+/− SE) swimming speed (**a**), variation in speed (**b**) and turning speed (**c**) of mosquitofish alone and in groups of 2, 4 and 8 (From Herbert-Read et al. (2013))

the timing of maintenance behaviour by group living animals has been overlooked. They showed that the proportion of preening birds at any given time increased with bird density and that preening behaviour appeared to be transmitted between neighbours. Such transmission is also known as contagion (Nicol 1995).

Another process affecting the behaviour of animals in groups is that of conformity. Conformity occurs when an individual performs the same behaviour as the majority of its group mates, or the commonest of the various behaviours that the group members are performing. One manifestation of conformity is that individuals can tend to copy the behaviour of the rest of the group even if alternative options are available, or doing so conflicts with their own personal preference. Guppies (*Poecilia reticulata*) have been shown to follow experienced group mates on long, circuitous routes to food patches, even when shorter alternatives exist (Laland and Williams 1998). Three-spined sticklebacks (*Gasterosteus aculeatus*) will join and forage with larger shoals, even when doing so means foraging in areas they had previously experienced to be relatively poor feeding grounds, and which, if foraging alone, they tend to spend less time in (Webster and Hart 2006b). Similarly, spice finches (*Lonchura punctulata*) that have been trained to expect one feeding area to be reliably productive will switch to a less profitable area if they see others using it (Rieucau and Giraldeau 2009).

Herbert-Read et al. (2013) compared the locomotory behaviour of individual mosquitofish when they were alone and when they were in groups of different sizes. They saw that individual fish had characteristic movement profiles when tested alone, but that as group size increased, this individuality disappeared as the fish tended to conform to the movement patterns of other group members. Remarkably, the fish adopted such group size-specific patterns of movement so that it was possible to accurately predict the size of group based on a knowledge of the movement characteristics of a single group member (Fig. 7.5). Some group members may be more plastic in their behaviour than others, and hence more likely to adapt their behaviour through conformity or facilitation. For example, Gouldian finches (*Erythrura gouldiae*) that have a bold behavioural phenotype tend to be less likely to conform to the patterns of behaviour shown by group mates compared to relatively more shy birds (King et al. 2015).

Pike and Laland (2010) showed that conformity can be frequency dependent, in that individuals can become disproportionately more likely to copy the behaviour of others as the number of group mates performing a behaviour increases. In their experiment, ninespine sticklebacks (*Pungitius pungitius*) were allowed to choose between two food patches that their group mates had fed at. They showed a preference for the food patch fed at by the majority of fish, a preference that grew with at a greater-than-linear rate as the number of foragers at the patch increased.

Taken together, research into the effects of facilitation and conformity suggest that these processes can have both quantitative effects upon group member behaviour, that is, changing the rate at which certain behaviours are performed, and also qualitative effects, with individuals in larger groups performing behaviours that they might not engage in if they were in smaller groups or alone.

7.6 Summary

In this chapter, we have seen that animal groups vary in size, under the influence of a range of different factors. There are good reasons for expecting group sizes in nature to exceed the theoretically predicted optimal size, the size that maximises the mean fitness payoff for the group's members, and Sibly's (1983) model provides useful framework for illustrating why this ought to be the case. In reality, there may well be no universal optimal size, since when we look at the level of each individual within the group, as opposed to the mean of all individuals, it is clear that the optimal size is likely to differ between them, and also over time. Given this, there is potential conflict between group members over the control of the size of the group and over the division of resources within it. Accordingly, group-living animals engage in a range of behaviours that influence group size and which in many cases have been shown, or more often inferred, to affect their fitness.

Collective Decision-Making

8

8.1 Introduction

Throughout the course of their lives, animals frequently have to differentiate between the various options available to them and to make decisions on a course of action. For those animals that live in groups, any decisions also usually involve the added dimension of the social context – a potential decision-maker usually has to account for the actions of other group members. While an individual may be motivated to take a particular course of action, if it does so unilaterally, it may break away from the rest of the group and thereby forfeit the benefits of social living. For this reason, animals in groups often have to make collective decisions, reconciling their own private information and motivations with those of other group members to arrive at some mutually satisfactory outcome. Typically, contexts for collective decisions include the timing of some group activity, or the travelling direction of the group, and a broad consensus is required among group members if they are to retain group coherence.

In recent times, considerable progress has been made in the understanding of social and collective behaviour in general, and in collective decision-making in particular. We can now examine animal groups both in terms of their microscopic, individual dynamics and their macroscopic, collective decisions. The process of making a collective decision in animal groups is fundamentally different to that which we envisage when thinking about human decisions. In human society, several potential options can be described and differentiated, and group members can each contribute by means of advocacy and discussion. By contrast, collective decisions in animal groups are achieved through more simple processes, yet, despite this, self-organised animal groups are often incredibly effective in arriving at collective decisions. While it may be imagined that the processes of integrating the disparate information held by multiple group members and then enacting some overall decision might be slow and prone to error, recent studies have exemplified the ability of animal collectives to make decisions that are both fast and accurate and to distinguish between multiple options to arrive at an optimal solution.

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8.2 Information Acquisition and Information Transfer

As described in previous chapters, individual animals obtain considerable benefits from being part of a group, for example, through more efficient foraging and enhanced abilities to detect and avoid predators. These benefits are founded on the greater access to information enjoyed by individuals in groups. Information could relate to any salient aspect of the biotic or abiotic environment, such as foraging opportunities, or levels of threat. It may be acquired by an individual through direct sampling of its environment, in which case the information is often referred to as private information. By being a member of a group, an animal may be able to enhance its rate of private information acquisition since certain behaviours are socially facilitated, such as in the case of exploration and predator inspection (Ward 2012). In addition, animals can gather information through the cues and signals provided by others in their environment. Social information, as this is known, is relatively inexpensive to acquire and permits individuals to access a broader range of information than they would be able to if they were to rely on collecting all of their information through direct experience.

For group-living animals, social information is a crucially important resource and may comprise the experience and information of all group members. The effective integration and application of this information is central to collective decision-making. Perhaps the most frequently used examples relating to the use of social information describe the ability of individuals in groups to locate food more rapidly than on their own (Giraldeau and Caraco 2000; Pitcher et al. 1982; Ward and Hart 2005). This improvement in foraging efficiency is driven by social information. A single individual searching for patchily distributed food has a relatively low probability per unit time of locating a food patch. But the probability of locating a food patch increases with the number of foragers. If each individual can monitor the other foragers and determine when they have located food – in other words, if it can use the available social information – it can join the finder at its food patch and increase its rate of food intake.

The transfer of social information between individuals forms the basis for collective behaviour. We can delineate two major categories of social information transfer: that which occurs by social signals and that which occurs by social cues. Signalling is an attempt by a signaller to influence the behaviour of a receiver, in this context, a deliberate effort to convey information by an informed signaller to a naïve receiver. By contrast, while cues also involve the transmission of information from one animal to another, they are inadvertent and not specifically evolved to communicate. Cues given out by an individual are interpreted by a receiver and are not typically an intentional means of communication by the cue giver. For example, in a foraging context, a pigeon pecking at the ground would likely provide a cue to an observer that it had located some food and was eating.

One of the best described forms of social signalling in this context is the honey bee's waggle dance (Seeley 1995; von Frisch 1967; see also Sect. 7.4). A foraging bee that has located a food patch communicates its finding to its nest mates by performing a dance upon its return to the hive. In the crucial phase of the dance, the bee vibrates its body and wings as it moves – it waggles – and the direction and duration of this waggle tells the observers the direction of the food patch, relative to the sun, and the distance to the food source (see Fig. 8.1). The process of information transfer by the waggle dance is not perfect, and foragers will often return to the nest having failed to locate the food patch in order to revisit the dance and to try again (Seeley and Towne 1992); nonetheless, signalling in this way does improve the efficiency of honey bee foraging under normal conditions (Dornhaus and Chittka 2004).

Honey bees are not the only animals that use signalling to facilitate information transfer. Ant trail networks are also a form of signalling, although the communication between individuals is indirect. Upon discovering a food source, an ant makes its way back to the nest, leaving small amounts of pheromone at intervals on its return journey (Hölldobler and Wilson 1990). This tends to recruit nearby ants to adjust their foraging behaviour such that they will tend to follow the initial trail. If they in turn find the food source, then they will navigate back to the nest, also leaving pheromone droplets in their wake. This establishes positive feedback and the trail becomes more attractive and recruits more ants. This positive feedback is limited both by the number of ants available to forage and by the fact that the pheromone contains volatile chemicals which evaporate over time, so the trail needs constant reinforcement if it is to be maintained. Moreover, the ants lay trails more intensively in response to higher quality food patches; hence, the network of trails around an ant nest is adjusted to not only the presence of food but the most profitable foraging patterns (Beauchamp 2014; Beckers et al. 1993; Portha et al. 2002). In a similar way to the ants, brown rats (*Rattus norvegicus*) are also known to create chemical trails connecting food sources to the nest, enabling nest mates to reduce the time taken to locate food (Galef and Buckley 1996; Galef and White 1997). Naked mole rats (*Heterocephalus glaber*) not only produce chemical trails but advertise their success in finding food to nest mates by using specific calls and by displaying food and waving it around (Judd and Sherman 1996). Some species of ants are also known to use more direct forms of signalling, such as tandem running, where an informed ant leads an uninformed nest mate from the nest to food, or to a new nest (Franks et al. 2009; Franks and Richardson 2006).

A version of the indirect information transfer used by ants in the formation and maintenance of trails is used to great effect by termite species in the construction of their nests. The uniting characteristic in both cases is that rather than responding directly to the actions of other group members, individuals adapt and modify their environment which in turn stimulates other group members to respond in a particular way (Moussaid et al. 2009). This indirect, or stigmergic, communication is perhaps exemplified best among termites which are able to construct huge nests without reference to a global plan, or even the need to be aware of other individuals (Grassé 1959). In the case of termites, the building process begins with an individual depositing a small amount of building material on the ground. The crucial aspect of this is that the building material contains pheromones which encourage subsequent termites to deposit their own pheromone-infused building material there. As the pile grows, its attractiveness increases through positive feedback, eventually leading in some species to the construction of the huge towers with which we are familiar (Beckers et al. 1994).

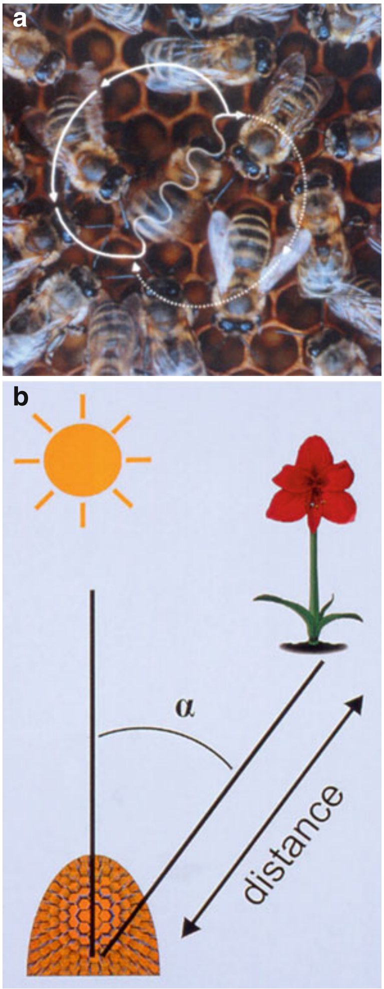

Fig. 8.1 (**a**) The waggle dance of the honey bee (*Apis mellifera*) provides information on the location of a foraging patch. (**b**) The angle of the 'waggle' corresponds to the direction, relative to the position of the sun (Figure design: J. Tautz and M. Kleinhenz, Beegroup Würzburg) (from Chittka 2004)

Like signals, cues allow a receiver to obtain information; however, cues are usually by-products of some aspect of an individual's behaviour, rather than an evolved attempt to communicate. An animal detecting a potentially threatening local stimulus will adjust its behaviour, for example, by turning away from that stimulus. The behavioural change in the detector is perceived by other group members nearby, who in turn adjust their own behaviour and the information spreads outwards from the source through positive feedback until, in some cases, it propagates throughout the entire group (Treherne and Foster 1981). As an example, a foraging bird may detect the approach of a predator and take flight, prompting the rest of the group to follow suit. There is some evidence to suggest that birds can differentiate between occasions when conspecifics take flight in response to a genuine threat, versus a simple departure from the area, which helps in minimising cascades of false alarms. Birds taking flight in response to a potential threat do so in a slightly different way to those taking off for other reasons, and this information can be used by other flock members to decide whether or not to take flight themselves (Davis 1975; Lima 1995). Upon taking flight, alarmed birds have a characteristically different trajectory to birds taking flight for other reasons. This may act as a cue in its own right; however, it may also produce audible cues which augment the basic information provided by them taking off and increase the likelihood of social transmission (Hingee and Magrath 2009). The crucial factor in all such cases is that although the predator may only have been detected by a small proportion of the group, by responding to social information, all group members take evasive action and are rewarded with their lives.

The process of information transfer between individuals can be extremely rapid and effective. A number of researchers described this process, notably including Breder (1954), who described ‘shock waves’ travelling across fish shoals, and Rashevsky (1951), a pioneer of mathematical biology, who discussed social imitation. However, it was Dmitrii Radakov (1973) who provided the greatest early insight to this phenomenon, quantifying the speed with which these waves travel across groups. In an experiment performed in an inlet of the Caribbean Sea in Cuba, Radokov induced fright responses in silversides (*Atherinomorus* sp.), a type of small shoaling fish, and filmed the reaction across the group. A small proportion of the group would be startled by the stimulus provided by Radakov and the behavioural response of these individuals would then transfer to their neighbours and from them in turn to their neighbours, such that a ‘wave of agitation’ would spread through the group. The speed of this wave was recorded at up to 15 ms^{-1}, which is far greater than the maximum swimming speed of any one individual, calculated at around 1 ms^{-1}. Crucially, the speed of transmission of information through the group is also typically faster than the speed of the predator to which the animals are reacting (Godin and Morgan 1985). Radakov also noted some interesting characteristics about these waves, including the fact that the wave propagated over a greater distance when the stimulus carried a greater threat, for example, when the school was attacked by a barracuda, but that the speed of propagation was similar in all cases. It was not clear from Radakov’s work what aspects of the behaviour of the initiators of these waves determined the distance over which the waves travel, or whether the propagation distance depends on the number of individuals that initially react to the stimulus. Nonetheless, the crucial contribution of Radakov was to demonstrate how collective behaviour can be achieved effectively purely through local interactions between individuals in a self-organising group. It is not necessary for the group response to be coordinated by a leader, nor for all individuals to be aware of the stimulus itself in order to respond effectively to it (Fig. 8.2).

To examine the question of why some waves propagate extensively through a group, while others fail to do so, Rosenthal and co-workers (2015) examined shoals of golden shiners. Periodically, a single fish would spontaneously perform a sudden

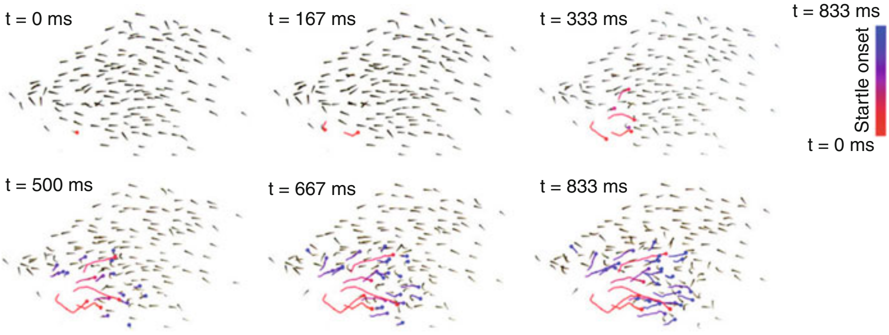

Fig. 8.2 Rosenthal and co-workers (2015) clearly showed the pattern of local information transfer between fish, beginning with a single fish a $t = 0$ ms, and radiating through that fish's near neighbour (From Rosenthal et al. (2015))

startle behaviour and the researchers could then examine whether and to what extent this would be transmitted through the group as a behavioural cascade. They found that the likelihood of a behavioural cascade propagating throughout a group as a result of an initial startle response was relatively low and that in fact most behavioural cascades attenuated relatively rapidly. The crucial question to address then is why do some startle responses propagate while others quickly die out? Rosenthal et al. found that simple measures such as the local density and number of near neighbours around the initiating fish had little effect on the likelihood of a response propagating. However, by constructing a sensory network of the shoal, based on the visual field of each individual, they were able to determine the sensory connections between each individual. Certain properties of these networks are vital in determining the probability of a startle event propagating. In particular, individuals with a high clustering coefficient in the sensory network, that is, those individuals who have a relatively high number of sensory connections with near neighbours who are themselves connected, have a high social influence on the group and are most likely to trigger a behavioural cascade. It also seems likely that waves are more likely to propagate when the animals within the group are in an alert state and so are more sensitive to perturbation (Bode et al 2010).

8.3 Collective Decision-Making

Group-living animals are frequently faced with decisions, selecting among multiple options that differ in terms of their costs and benefits. The decisions typically relate to spatially discrete alternatives, such as the choice of a group travelling direction or the selection of a new shelter by ants, *Temnothorax albipennis* (Franks et al. 2003b), or the decision over the timing of a particular activity, for example, the decision to move from a resting site in animals such as primates (Petit and Bon 2010). In choosing among the available options, social information is crucial. If group members are able to identify which individuals have pertinent information and to copy the decision of those individuals, then high-quality information is transferred and decisions can be improved across the whole group. If the animals are to maintain the benefits of grouping, then the decision should be adopted by all group members. Instances where group members arrive at a unanimous decision while maintaining group cohesion are often referred to as consensus decisions (Conradt and Roper 2005).

A characteristic of consensus decisions is that when faced with a binary choice between two identical options, one will be chosen at random. If the same scenario is presented repeatedly, this will lead to a clear U-shaped distribution of choices, where the probability that the entire group opts for one or other option is very high, and consequently the probability that it splits between the two options is low (Camazine et al. 2001; Deneubourg and Goss 1989; Deneubourg et al. 2002). This situation has been examined many times, for example, using cockroaches (*Blatella germanica*), which were given a choice between two resting sites, and using tent caterpillars (*Malacosoma* spp.), which were given a choice between two similar food sources (Ame et al. 2004; Dussutour et al. 2007). In both cases, an initial, random choice is amplified by positive feedback.

But while such situations present a valuable opportunity to examine collective decision-making in a simplified context, the decisions that animals take in the real world are often much more complex than this. For example, to forage effectively, ant colonies often need to exploit multiple ephemeral food patches simultaneously. In such situations, the formation of foraging trails represents a highly responsive collective, and dynamic, solution to resource gathering in an ever-changing environment. Generally speaking, most decision-making scenarios involve a choice between mutually exclusive alternatives, which differ in their profitability. The ability of animals to arrive at consensus decisions in these circumstances raises the question of how they are able to collectively integrate information and decide on a preferred option among multiple alternatives.

To answer this, it may be necessary to differentiate between collective decisions taken across different taxa. The ability and the tendency to communicate across the group changes the dynamics of the decision-making process. In large groups, such as in bird flocks, fish shoals and social insect swarms, no single individual may typically be able to communicate directly with the entire group and consequently no individual can monopolise the decision-making process. Instead, the decision emerges through self-organisation. By contrast, decision-making in smaller groups, such as those formed by some species of mammals, including primates, cetaceans and some ungulates, can be a rather different process, as a single individual can communicate with the entire group, leading to greater possibilities of negotiation and voting and shaping patterns of following and leadership (Conradt and Roper 2005). We suggest that it may be useful to consider decision-making mechanisms in groups where communication between group members is predominantly local separately to the mechanisms underlying decision-making in groups where global communication is possible. In saying this, we acknowledge that these categories need not necessarily be mutually exclusive, indeed there are many instances where both mechanisms are involved.

8.3.1 Mechanisms for Consensus Decision-Making Based on Local Communication

Collective decision-making may seem to imply some form of consultation between group members, but that is not the case for the majority of animals that live in groups. Instead, self-organisation based purely on local interactions provides an excellent means of decision-making. Each group member will generally have the ability to detect its own local environment and bases its behaviour on cues arising from its near neighbours, particularly their position, orientation, speed and acceleration. If an individual initiates a new movement direction, this may be amplified through positive feedback until the group is recruited to the move. If more than one option is available, the one that is amplified the quickest is the one that will ultimately be selected by the group. Generally speaking, the option that is preferred by the majority will tend to be amplified the most quickly. This process in large groups of animals was modelled by Couzin et al. (2005), where the group contained individuals that preferred one of two travelling directions. If the angular difference between the two travelling directions was small, the group would tend to average the travelling direction between the two options as a result of the tendency of the animals to remain with the group. If the difference in the directional preference was too great, the group would switch to travel in the direction that was preferred by a majority of group members. The decision-making process here arrives at a consensus without the need for group members to have complex cognitive abilities, or a global perspective of different individuals' preferences. An experimental test of this prediction was made using homing pigeons (*Columba livia*) by Biro and co-workers (2006), who trained individuals to return to their loft from different release sites. Over time, each bird developed its own individual route preference. Next, the researchers released the pigeons in pairs. As predicted by Couzin et al.'s model, when there was little difference in the directional preferences of the two birds, they tended to follow the average of their directional preferences, each responding to the information about the other's trajectory (Pettit et al. 2013). When the difference between the two birds' preferences became too great, the pair either split, or one individual compromised so that it simply followed the other. In these cases, conflicts are resolved simply through the application of basic interaction rules. Moreover, recent theoretical model approaches suggest that rather than damaging the ability of groups to make effective decisions, conflict may actually even enhance the process (Conradt 2013; Conradt et al. 2013).

Another crucial aspect of Couzin's model was that it shows that the larger the group, the smaller is the total proportion of informed individuals required to

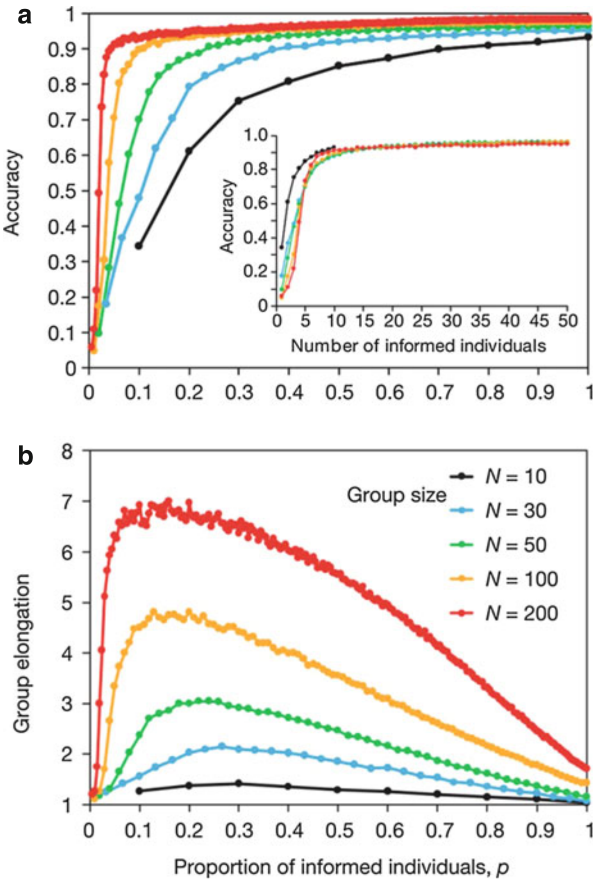

Fig. 8.3 (**a**) As group size increases, the proportion of informed individuals required to lead a group decreases. (**b**) The proportion of informed individuals also affects group morphology. When there is a low proportion of informed individuals, groups tend to be elongated, as the informed leaders adopt positions at the front of the group and the remainder of the group follows (From Couzin et al. (2005))

effectively lead the group (Couzin et al. 2005). The model indicates that around 20 % of group members are required to lead groups of 50, whereas in groups of 200, less than 5 % of the group can effectively lead (see Fig. 8.3). One explanation for this is that the frequency of interactions between individuals is greater in larger groups, so information propagates more rapidly. Moreover, these informed individuals are able to shape the movement patterns of the group as a whole without any form of signalling; leadership emerges as these individuals balance their attraction to the target location against their attraction to near neighbours. This finding means that relatively few informed individuals with a directional preference can shape the movement patterns of large numbers of conspecifics. This fascinating aspect helps to explain how large groups of animals manage to navigate effectively. If naïve individuals have no strong preference for a travelling direction, as in the previous example, then they will be easier to lead. Subsequent work by Conradt et al. (2009) suggests that group members who hold pertinent information on, for example, the location of a foraging patch may be able to increase their influence on the group by making slight adjustments in behavioural parameters, such as increasing their speed

Fig. 8.4 Tandem running in ants. The follower maintains antennal contact with the leader (Picture copyright Stephen Pratt)

and reducing the strength of their response to group mates (Gueron et al. 1996). Yet it would be wrong to classify those naïve individuals, or those without any strong preferences for group travelling direction, as being unimportant to the decision process. Theoretical models have suggested that increasing the numbers of these uninformed individuals in a group tends to increase the probability that the group will arrive at a consensus (Leonard et al. 2012). Furthermore, the presence of increasing numbers of uninformed individuals has a stabilising effect on collective decision-making. By increasing the absolute number of individuals in the group, the influence of highly motivated minorities is reduced, which tends to promote the adoption of less strongly held, but more widespread, directional preferences by the group as a whole (Couzin et al. 2011).

Positive feedback is an essential component of collective decision-making; however, if it is entirely unfettered, the result can be a potentially disastrous informational cascade, with serious consequences for all group members. In order to minimise the risk of this happening, group members may apply a simple decision rule, such as a quorum response, which describes how an animal's probability of performing a behaviour is a non-linear function of the number of other individuals already exhibiting this behaviour. This allows the collective response to be tuned through both positive and negative feedback. The quorum response operates by initially suppressing the propensity of individuals to follow a new initiative until a minimum threshold number, or quorum is reached. Once this occurs, the probability of individuals to follow this initiative increases sharply (Sumpter and Pratt 2009; see Fig. 8.4). This non-linear functional response to the novel social information reduces the likelihood of 'blind copying' – the uptake of poor information – because it limits the influence of misinformed individuals on the behaviour of the group as a whole. Although quorum mechanisms cannot fully exclude the risk of informational cascades (Dall et al. 2005; Laland and Williams 1998), on average they outperform the alternatives where animals place no, or low, reliance on social information. The quorum rule has been shown to be important in mediating collective decisions in contexts including predator detection and foraging and across a range of different species (Collins and Sumpter 2007; Pratt 2005; Seeley and Visscher 2004; Ward et al. 2008b, 2011).

Quorum mechanisms provide a powerful means of comparing between different options, allowing individuals an opportunity to gauge the preferences of other group members. Other mechanisms of weighing social information have been proposed, for example, simple comparisons based on an observation of the absolute number of group members that have already decided on each of two options or a comparison of the relative difference between the two factions based on Weber's law. Arganda and co-workers (2012) proposed a mathematical rule based on Bayesian estimation which may provide a mechanism that unites these various different means of comparison, allowing animals to select between two different options and thereby to make effective collective decisions.

8.3.2 Mechanisms for Consensus Decision-Making Based on Global Communication

The dynamics of decision-making when group members are able to communicate across a large proportion of the group, or even globally, have been studied extensively, partly in reference to a perceived similarity to human decision-making processes (Conradt and List 2009). The analogy rests with the ability of animals in these situations to communicate their intentions in a manner likened to voting that allows group members to assess the relative strength of different preferences and factions within a group. There are often characteristic behaviours that occur in the build-up to a group move, including communication between group members (Petit and Bon 2010). The communication in this case may relate to the timing and direction of collective movements. The purpose of this pre-departure communication is most likely to try to build consensus and avoid fracturing the group. Several different forms of this intra-group communication exist. Primates, including gorillas (*Gorilla gorilla*), vocalise to inform other group members of their intention to move (Stewart and Harcourt 1994). Boinski and Campbell (1995) studied vocalisations, and the responses to vocalisations, among troops of white-faced capuchins (*Cebus capucinus*). They found that individuals at the front of groups vocalised more frequently, which assisted in initiating new movements and increasing coordination in existing troop movements. Communications of intent can be achieved by aspects of behaviour; yellow baboons (*Papio cynocephalus*) orient their bodies in the direction of some goal prior to moving off. When large numbers of adults in the troop orient in a similar direction, this indicates their direction of preferences and their readiness to begin a collective movement (Norton 1986). A less specific, but more widespread phenomenon is a build-up in activity prior to a collective movement, as seen in sheep, cattle, swans and fish (Black 1988; Ramseyer et al. 2009a; Ramseyer et al. 2009b; Ward et al. 2013). In all these cases, communication during the pre-movement phase facilitates the achievement of consensus over the timing of a collective movement and, in some cases, consensus over the direction as well, by establishing the relative proportions of group members who are committed to a given course of action (Calf et al. 2002; Petit and Bon 2010).

The ability of animals to implement their own preferences and decisions can be constrained by their membership of a group (Norton 1986). So, while the term consensus decision-making implies that all individuals contribute to a decision and that there is little conflict, this is not necessarily the case. The decisions may be made by a single individual, or a small subset of individuals. Group members who find that their preferences are not well matched by the decision are forced to make the choice of either separating from the group, and thereby lose the benefits associated with grouping, or to remain with the group and pay a so-called consensus cost (Conradt and Roper 2005). Alternatively, a large proportion of the group may contribute to each decision, in which case the outcome likely reflects the desires of the majority of the group more accurately. As well as providing a more equitable solution for all group members, shared decisions may allow information pooling and, potentially, better decisions (List 2004). These shared decisions are sometimes characterised by voting behaviour. One celebrated example of this is provided by herds of up to 1000 African buffalo (*Syncerus caffer*) when they move off from their resting grounds to forage each evening (Prins 1996). The adult female members of the herd are the ones who vote and each expresses her preference by standing and gazing in a particular direction. Prins estimated the mean direction of gaze prior to the herd's departure and found that when they moved off, they did so in that direction. Furthermore, the herd achieved something close to consensus as there was usually a direction that was preferred by a large proportion of the group and this was the direction taken. Hence, the buffalo coordinate their directional preferences by a means which takes into account the information of the experienced adult females. Voting has also been described in primates, such as baboons (*Papio cynocephalus*) (Norton 1986) and Tonkean macaques (*Macaca tonkeana*), which must make foraging decisions regarding which fruit trees to move to in the forests where they live. The process begins with an individual indicating its preferred direction by travelling a short distance in that direction, then pausing to look back at the group. If another individual then proposes an alternative course, the troop then votes as each individual moves towards its preferred candidate, again stopping to look back at the rest of the group. The voting process is not entirely unconstrained, but is influenced by selective mimetism, as individuals tend to support those with whom they have the closest affiliations (Fletcher 2009). Once a majority has settled on one of the options, then the remaining undecided individuals and those that originally supported the less popular option join the majority and the group's selection is made (Sueur and Petit 2008a, b; Sueur et al. 2009, 2010). In a recent study of collective decision-making in a troop of olive baboons (*Papio anubis*), Strandberg-Peshkin and co-workers (2015) examined the patterns of decision-making against the level of conflict over direction. When the difference between proposed routes was relatively small, the troop tended to compromise, moving in a direction which was near the average of the alternative routes. However, when the difference was greater, the troop achieved consensus by opting for the route proposed by the most initiators. The decision-making patterns exhibited by the baboons align closely with the theoretical predictions made by Couzin et al. (2005).

8.3.3 Quorums and Consensus Decisions for Nest Sites in Social Insects

The process of choosing a new nest has been studied extensively in social insects, particularly in bees and ants, and is perhaps the exemplar of animal collective decision-making. In both cases, mechanisms exist to communicate directly the different options available and then to choose the best option on a majority basis. In good years, honey bee (*Apis mellifera*) colonies can grow to the point where they become too large for their nest. If this happens, the founding queen will leave the colony to seek a new nest, taking around three-quarters of the workers with her (Rangel et al. 2013; Rangel and Seeley 2012). This transitional group will then adopt a temporary home, often on a tree, while about 5 % of the group leave to investigate potential places to site a new nest. On their return to the group, these scouts produce a waggle dance to communicate the location of the nest site. Initially, there may be several scouts dancing, each advocating its own choice, but over periods that can last from a few hours up to a few days, some scouts stop dancing. These bees may then either independently discover another site, or be recruited to advocate another's choice until gradually the number of bees advocating a given nest reaches a quorum (Seeley and Visscher 2003). The dancing of the scouts provides information on the quality of a site and has the effect of recruiting additional scouts to inspect the site. If they find it to be a good site, they too will advocate this option by producing a waggle dance (Seeley 2010; Seeley and Visscher 2008). Once the number of scouts recruited to a particular nest site reaches a quorum, those scouts produce stop signals to inhibit scouts dancing for other sites, or even interfere with their dancing by butting them (Seeley et al. 2012). It is this negative feedback which is largely responsible for the ability of bees to break deadlocks when they have a small number of appropriate sites. A similar 'stop' signal is given during honey bee foraging when a forager returns to the nest having been attacked at a feeding site to prevent waggle dances from continuing to recruit to that feeding site (Nieh 2010).

Once a new nest site has been decided, the scouts begin to make a vibrational, piping signal to prepare workers to ready themselves for flight. Even at the stage when the swarm begins to move, however, only a relatively small proportion of the group know the location of the nest. The rest are guided there by the informed scouts who 'streak' – travel at high speed – though the upper layers of the moving swarm in the direction of the new nest site (Beekman et al. 2006; Schultz et al. 2008). This transmits information to the bees nearby and enables them to move in the correct direction. Once a streaker reaches the front of the swarm, it slows and returns to the back of the swarm before repeating the streak, and with multiple streakers performing the behaviour, the swarm can be guided to the new nest.

The process of nest-site selection in ants has been studied extensively in rock ants (*Temnothorax albipennis*). Like the honey bees described above, the ants are able to decide among several options for a new nest. The ants live in comparatively small colonies typically with fewer than 200 workers inside rock fissures. These nest sites are considered to be ephemeral in nature, so the ants often have to search for and decide upon suitable new nest sites. When it becomes necessary for the ants to relocate the nest, up to a third of the colony members begin to scout for alternatives in the vicinity (Pratt et al. 2002). Once a scout finds a candidate nest site, it makes an assessment according to multiple criteria including size, cleanliness, the number of entrances and the presence of conspecific nest sites in the area (Franks et al. 2003b, 2005, 2006, 2007). Given the possibility of several competing alternative nest sites, a strategy that involves making a direct comparison of all alternatives may be slow and inefficient. Instead, ants appear to apply a simple rule, selecting a nest site if it exceeds a quality threshold (Robinson et al. 2011). Once it has decided in favour of a nest, the scouting ant will then start to recruit additional scouts to the site, guiding one ant at a time through tandem running (Franks et al. 2009; Franks and Richardson 2006; Möglich and Hölldobler 1974; see Fig. 8.4). Once this newly recruited scout arrives at the nest, it too will make an assessment of the nest. If it in turn finds the nest to be suitable, it will also recruit and positive feedback begins. The ants are able to use tactile cues to estimate the number of ants at the new nest site. If this number is above a threshold, the decision is effectively made and the ants switch tactics to begin a phase of social carrying, where they start to carry remaining adults and the brood to the new site (Franks et al. 2003a; Pratt 2005; Pratt et al. 2002).

The mechanisms used by social insects to achieve consensus when more than one option is available are simple and typically produce accurate results. There is however a potential trade-off between the speed of a decision and the accuracy of that decision in the nest-site selection context for social insects (Franks et al. 2003a). Greater accuracy may require a larger number of scouts, which slows down the decision. If the insects need to reach a rapid decision, however, they are able to adjust their behaviour by restricting the number of individuals required to make the decision. In addition, while different options may exist where social insects begin to select nest sites, the inclusive fitness costs of making slow and/or inaccurate decisions mean that the likelihood of conflict is low (Bourke and Franks 1995). The beguiling simplicity and efficiency of the self-organised processes used by social insects in making decisions have inspired optimisation algorithms that are being used in human endeavours, including computing, artificial intelligence and robotics.

8.4 Decision-Making and Leadership

A crucially important consideration in the study of collective decision-making is that of leadership. This can refer to the position of an individual at the front of a moving group, or an individual who is the initiator of a change in group behaviour. These are not the same, however, and are subject to different constraints (Krause et al. 2000); hence, in this context, we refer to leadership as the initiation of transitions in group behaviour. Collective decision-making has been studied most extensively in the context of collective movements, where multiple individuals travel synchronously and coherently as a group between two points (Ward et al. 2013). The decision of the group is manifest as a change in behaviour, often this is exemplified in either a collective transition between a stationary phase and a moving phase, or a change of direction in an existing group movement. The outcome of the decision can be determined easily as each group movement will tend to have a leader (or a small group of leaders), the one who successfully initiates a group movement (King 2010). It is usually inferred that this individual is the decision-maker, so that leadership and decision-making are synonymous. This represents a simplification in some instances, however. While leadership implies a centralised form of decision-making, the emergence of a leader is often only possible following a period of consensus building in the group which is vital to maintain the coherence of the group and therefore the benefits of group living. For example, in groups where global communication is possible, when an individual initiates a new group movement, the decision to move may have been made by the group before the initiation took place during the crucial predeparture phase, as is the case with many primates, including gorillas (Stewart and Harcourt 1994). By contrast, in groups where communication is local, the decision-making process does not generally begin until an initiation attempt is made and group members decide whether to recruit to the new initiative (Ward et al. 2008b).

8.4.1 Who Decides?

Unshared decisions, or partially shared decisions, occur when only a single individual or a subset of the social group contributes to the decision-making process. Those who make the decisions gain benefits including obtaining greater control of when the group moves, and in which direction, whereas those who do not, or cannot, contribute to decision-making face the choice between remaining with the group and paying a so-called consensus cost, in particular taking part in a group move at a time or in a direction that is not optimal for them (Conradt and Roper 2005; Erhart and Overdorff 1999), or leaving the group and foregoing the advantages of sociality. Generally, if levels of conflict are low, and the benefits of grouping are high, then consensus costs will be correspondingly low and there is little risk of the group splitting. As conflict between the preferences of different factions within the group increases, the consensus costs and the likelihood of the group splitting also increase (Conradt and Roper 2009). Kerth and colleagues (2006) studied the role of conflict in precipitating the splitting of groups in the context of roosting decisions in Bechstein's bats (*Myotis bechsteinii*) by manipulating the experiences of the bats at some roosts. Although the bats took group decisions on roost locations, conflicting information over roost-site suitability led to a greater likelihood of group fission.

Broadly there are two main categories that have been investigated as potential determinants of who decides and who does not. First, the identity of a decision-maker may be important, and in particular, dominant individuals may be expected to play a greater role in the process than group members that are subordinate. Second, the state of an individual may be the key to determining who decides. For example, those that have the highest motivation – often those that have the greatest need to acquire resources – tend to be most likely to monopolise decision-making in the group. Motivation may also be influenced by the information held by a group member, and typically the most informed individuals should be expected to contribute most to decisions. In addition, individuals with bold personality types tend to contribute disproportionately to decision-making, possibly through social indifference (Conradt and Roper 2009). These factors are interlinked to an extent. For example, older individuals tend to hold more information and are also more likely to be socially dominant. Which factors are most important vary from species to species and across contexts.

8.4.1.1 Individual Identity: Social Dominance and Leadership

Considerable research has been carried out into the question of whether socially dominant individuals in hierarchical groups tend to monopolise the decision-making process. The findings have shown considerable differences between species. For example, in several species of social carnivores that form dominance hierarchies, such as dwarf mongooses (*Helogale parvula*), meerkats (*Suricata suricatta*) and golden jackals (*Canis aureus*) (Holekamp et al. 2000), the likelihood of successfully initiating a group movement is predicted by the social dominance of an individual. This may be through active manipulation of subordinate group members, or because the subordinate individuals are especially attentive to the behaviour of the dominant, or because they are more likely to respond to a movement initiation by a dominant individual, so-called selective mimetism (Sueur et al. 2009). In other species, such as wolves (*Canis lupus*), there exists a strong hierarchy, but according to several authors, this does not lead to consistent dominance of movement decisions by the alpha male (Fox 1972; Mech 1970); thus, such decisions in wolf packs are at least partially shared. Among primates, dominant individuals may also monopolise the decision-making process, but the extent to which they do this varies between species, from gorillas, where the silverback male almost always leads group movements (Watts 2000), to Barbary macaques (*Macaca sylvanus*), where dominance is certainly an important factor in group decision-making, but not the only factor (Seltmann et al. 2013), to white-faced capuchins (*Cebus capucinus*), where dominance has no clear effect on decision-making (Leca et al. 2003). To complicate matters, it can be difficult for human observers to resolve who leads. Often researchers opt to simply record the first individual to move and whether that individual was followed. However, this disregards the critical stage preceding the initiation, during which individuals may communicate their preferences and readiness (Petit and Bon 2010). To return to the example of gorillas, although the male leads group movements, there is a build-up of vocalisations among the group in the lead up to the move and these could serve to communicate the readiness of group members to move, hence what appears to be a decision that is enforced on the group by the silverback may in fact be shared (Stewart and Harcourt 1994). The relationship between the social hierarchy and leadership in moving groups was also described in elegant studies on pigeons by Nagy and colleagues (2010, 2013; see Fig. 8.5). Birds were fitted with a GPS device, allowing a detailed understanding of the interactions between individuals when the flock was in flight. The data revealed that although pigeons have strict social dominance hierarchies, the patterns of leader-follower relationships in moving flocks were independent of this, potentially allowing individuals with relevant experience or information to lead a flock, rather than relying on dominant but possibly ill-informed individuals. Similarly, a study on the collective movements of

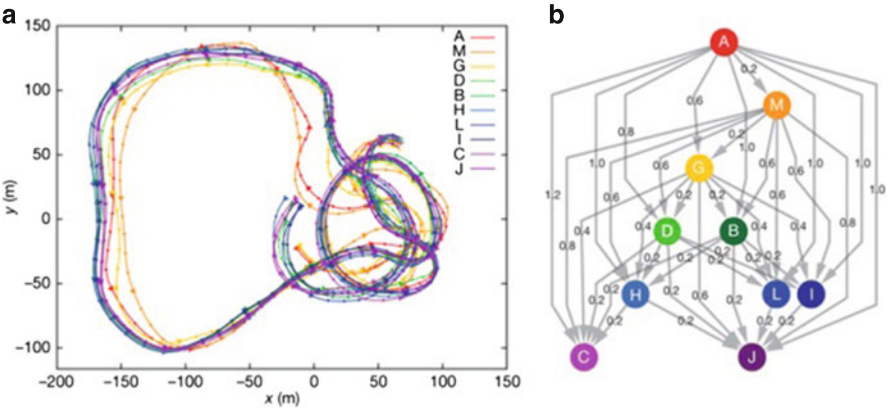

Fig. 8.5 (**a**) The tracks of ten pigeons (*A–J*) in flight over a two-minute period. (**b**) From this data, Nagy et al. (2010) constructed a hierarchical leadership network. Each pair of birds is connected by an *arrow*; in each case, the *arrow* points from the leader to the follower, and the value in each case gives the time delay of the response of the follower to the leader's trajectory (From Nagy et al. 2010)

free-ranging olive baboons showed that despite the existence of a structured social hierarchy in this species, decisions over the direction of travel were shared among the members of the troop (Strandburg-Peshkin et al. 2015).

In some cases, the extent to which dominant individuals monopolise group decision-making can reflect the importance of a hierarchy in the social organisation of the species in question. Sueur and Petit (2008b) used a comparative approach to examine consensus decision-making relating to group departures in two closely related primate species, the Tonkean macaque (*Macaca tonkeana*) and the rhesus macaque (*Macaca mulatta*), taking into account the behaviour of the group prior to departure. The social organisation of the Tonkean macaque is less hierarchical than that of the rhesus macaque, and this appears to be reflected in the extent to which decisions are shared among group members between the two species, with much greater sharing of the decision in Tonkean macaques, while dominant troop members played a disproportionate role in rhesus macaques. The stability of group membership also plays an important role. In ruffed lemurs (*Varecia variegata*), dominant individuals seem to emerge as leaders when group composition is stable, but they have lower influence in less stable groups (Overdorff et al. 2005). Overall, it seems that social dominance may skew the influence of high-ranking individuals in group decision-making, but that the extent of the skew varies considerably across species, and the true nature of the decision may rest in subtle communications prior to the execution of that decision.

8.4.1.2 Individual State: Motivation, Information and Leadership

Groups are often composed of individuals that differ at any given point in time according to their internal state. The internal state of an animal may refer to many different things; however, the most relevant here are the individual's physiological state and the information that it holds. These in turn affect an individual's motivation to influence the group decision-making process; more motivated individuals are likely to be more assertive. When a social animal feels a powerful imperative to move towards a given target, this may often result in it assuming leadership of the group albeit without necessarily having a preference for doing so. This phenomenon is sometimes referred to as leading according to need (Conradt et al. 2009; Rands et al. 2003). In such cases, leadership emerges through self-organisation, as motivated individuals increase their speed (Gueron et al. 1996) and gradually move to the front of the group, where they exert greater influence over the travelling direction.

Since accurate decision-making relies on using information to select the best available option, informed individuals should play a major role in the decision-making process. A number of studies have shown that informed individuals are able to act as leaders in groups. In shoals of golden shiners comprising individuals with information about the timing and location of foraging opportunities, and other group members who were naïve, the informed fish adopted positions at the front of the group and led the group towards the food. In the process, the naïve fish not only gained a foraging opportunity, but were also able to learn to access these opportunities themselves (Reebs 2000, 2001). Animals may learn local travel routes within their home ranges, such as the locations and most direct way to get to different prey patches. In a laboratory study of guppies, Laland and Williams (1997) showed that naïve guppies could learn to navigate simple mazes by swimming with trained shoal mates. Moreover, guppies acquired this information so readily that even when experienced individuals were successively replaced with new, naïve fish, the group still used the original travel route that they had learned from their more experienced – and now absent – shoal mates, even though alternative routes of equal length were available, and even when all of the trained 'founder' fish had been removed from the group. In fact, this model system was also used to highlight one of the drawbacks of relying too heavily on social information; guppies persisted in using the travel routes that they had learned from their shoal mates even after shorter routes were made available to them (Laland and Williams 1998).

As well as learning about local travel routes, there is evidence that some animals can learn migration routes that cover far greater distances. In whooping cranes (*Grus americana*), young birds migrating for the first time from Wisconsin to Florida in the USA took more direct routes, with fewer deviations, if they were travelling in groups that contained older, experienced birds than they did if travelling by themselves. Travelling with group mates with previous migrating experience improved the migratory accuracy of young naïve birds by nearly 40 % (Mueller et al. 2013; see Fig. 8.6).

A similar pattern of leadership by informed individuals was recorded by Helfman and Schultz (1984) in French grunts (*Haemulon flavolineatum*) travelling along a daily migration route; naïve individuals also showed evidence of having socially learned the route in a short space of time. Most experimental investigations of the role of informational status in determining leadership tend to pair informed and uninformed individuals, so that there is a large difference between group members in the information held. Using pigeons, Flack et al. (2012) were able to take a more

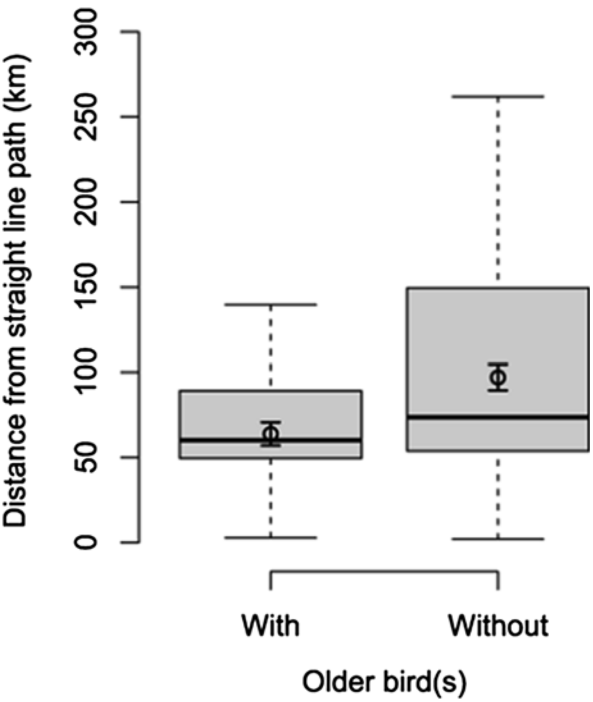

Fig. 8.6 Young whooping cranes that were accompanying older, experienced cranes followed a less tortuous path on their first migration from Wisconsin to Florida compared to those that were travelling without experienced flock mates (From Mueller et al. (2013))

nuanced approach where there was a difference in knowledge between animals, but without using the binary informed versus uninformed approach. They manipulated the level of experience that different birds had with a given route and then examined patterns of leadership between pairs of birds travelling along that route. As predicted, they found that those with greater experience tended to lead but also that the magnitude of the difference in the informational status between the two birds determined the probability that the more experienced bird would lead. In larger groups, the balancing of both personal information and the need to maintain social cohesion tends to lead to consensus decisions (Miller et al. 2013).

This trade-off is likely to exist for most group-living animals, as being too assertive in the process of initiating a group movement or changing the course of an existing movement could lead to the isolation of that individual, so each has to reconcile its degree of assertiveness with its desire to remain with the group. A study by Ioannou and co-workers examined this balancing act in shoals of golden shiners. Within these shoals, some fish had information on the location of a potential food patch, and so were motivated to travel towards that patch, while others lacked this information. Informed fish moved towards their goal, but the rate at which they did so determined whether the uninformed fish followed, with the fastest, most direct individuals tending to leave the rest of the group behind. Those informed individuals that led the group effectively travelled more slowly, appearing to balance their motivation to reach the goal against their motivation to maintain social cohesion with the other members of the group (Ioannou et al. 2015).

Differences in energetic requirements between the members of a group can be an important driver of positioning behaviour. Some individuals may have consistently greater energetic demands than other group members and are consequently likely to emerge as leaders. This might be for any one of a variety of different reasons: these may be individuals who deplete their resources more rapidly due to higher metabolic demands, or due to their parasite load, or because they have less capacity for storage, or are less effective foragers. Such individuals have the greater immediate need to acquire resources, so expediency may drive the collective decision-making process. In addition, the need to move to acquire resources may correlate with dominance since dominant animals are often the largest members of their groups, and so have the greatest absolute energy requirements (Sueur et al. 2013). In ungulates, such as the plains zebra (*Equus burchellii*), pregnant and lactating females often initiate group movements as they have relatively higher energy intake requirements and also need to obtain more water for milk production (Fischhoff et al. 2007).

In other cases, energetic differences among group members may reflect shorter-term variance in food intake. Hungry individuals in shoals of roach (*Rutilus rutilus*) adopted positions at the front of the group where foraging opportunities tend to be greater. They remained in the leading positions until they gradually became sated and were supplanted by hungrier individuals (Krause 1993b). These position changes can be replicated by state-dependent adjustments of behavioural parameters. Travelling speed is one such parameter. Hungry individuals tend to travel more quickly and so may assume positions at the front of groups (Hansen et al. 2015a). However, even in cases where hungry animals do not travel more quickly, they may still be found towards the front of groups, relative to the position of satiated group members. The mechanism is less clear in this instance, but one possibility is that differences in interindividual spacing behaviour between hungry and satiated animals contribute to this pattern, with hungry individuals tending to move away from conspecifics (Hansen et al. 2015b).

8.4.2 Leadership and Animal Personality

Research across a wide range of species has revealed the existence of consistent interindividual differences, or personalities, among animals. These differences are manifest in a range of contexts, and in many cases, different behaviours are correlated, such that they form behavioural syndromes (Sih et al. 2004a, b). There can be considerable variation across individuals within a population in terms of their sociability. In addition, sociality often forms part of a syndrome with boldness and activity, so that highly social animals are generally less bold (often termed ‘shy’) when faced with risk and are typically less active in open field tests. By contrast, less social animals are often relatively bold and are highly active and exploratory. In regard to the relationship of personality and behavioural syndromes to the dynamics of grouping behaviour, and specifically to leadership, bolder, more active and less social individuals tend to emerge as leaders (Jolles et al. 2015; Kurvers et al. 2009; Ward et al. 2004b). This was examined further by Harcourt et al. (2009) who found that bold individuals were more likely to initiate movements, while shy individuals showed less initiative, but had a strong tendency to follow. The coexistence of bold and shy animals in groups may ultimately be of benefit to all group members, since it potentially allows greater flexibility in collective decision-making and ultimately more efficient foraging (Dyer et al. 2008; Michelena et al. 2009). Fully explaining the role of personality in determining leadership may require that a distinction be made between alternative hypotheses. In this context, the social indifference hypothesis would suggest that bold individuals weight their desire to travel towards a given destination above the need to remain with the group and so ultimately end up leading the group (Conradt et al. 2009). By contrast, the leading-according-to-need hypothesis (Conradt et al. 2009) would suggest here that if bold individuals are subject to greater relative energetic or physiological demands, this might predispose them to act as leaders. At this time, the extent to which individual differences in behaviour relate to individual differences in metabolism or energy expenditure is a topic of debate (Careau and Garland 2015; Mathot and Dingemanse 2015a, b). While the majority of studies have reported a positive correlation between aspects of personality and the underlying physiology, the evidence is not unequivocal (see Mathot and Dingemanse 2015a for a review). Added difficulties in assessing the status of this field of research include the possibility of a publication bias, which militates against the reporting of null results, and the existence of many different measures of metabolic rate and energy expenditure. Moreover, studies often emphasise a causal relationship, rather than a more nuanced coadaptation of physiology and behaviour involving sometimes complex feedbacks between these and the environment of the animal. Further research is merited into this fascinating area, and the review and prospectus provided recently by Sih et al. (2015) provides an excellent path to a broader understanding.

8.5 The Functional Benefits of Collective Decision-Making: How Good Are Collective Decisions?

Many animals are able to achieve far more as part of a collective than they might if they were to live independently. Nowhere is this synergism demonstrated better than through the phenomenon of collective decision-making. The ability of groups to be more than the sum of their parts in this respect is sometimes referred to as swarm intelligence, or the wisdom of the crowd. Swarm intelligence was formally defined by Krause and can be said to occur where individuals independently acquire information; the information of many individuals is in some way processed and integrated through social interaction leading to a collective solution to a cognitive problem that could not be implemented by isolated individuals (Krause et al. 2010). The most famous early example of this was Galton's (1907) description of a competition held at a country fair in England to guess the weight of the butchered carcass of an ox. A little less than 800 people submitted a guess with the hope of winning a prize on offer for the most accurate. There was considerable – and very important – variation among these guesses. Both the mean and the median of these guesses were startlingly accurate, especially the mean, which differed by less than half a kilogram from the actual weight of the carcass, 545 kg. Put in a different way, the crowd of guessers collectively 'knew' the weight of the ox carcass. Human crowds are by no means the only examples of a system in which the ability of the collective to make good decisions is greater than that of individual group members. In a study on the ability of mosquitofish (*Gambusia holbrooki*) to detect and avoid a replica predator in a Y-maze, Ward et al. (2011) reported that solitary fish avoided the arm of the maze containing the replica around 56 % of the time, in other words, little better that the null expectation in a Y-maze of 50 % of the time. Furthermore, these single fish not only made inaccurate decisions much of the time, but they were also slow to make those decisions. By contrast, fish in groups showed dramatic improvements in both decision accuracy and speed, with fish in groups of 8 and 16 selecting the correct arm of the maze approximately 85 % of the time and able to make decisions in less than half the time of the single fish. Groups also have an advantage over isolated individuals in terms of detecting cues in the environment (Grunbaum 1998). This was tested in another fish study, this time using golden shiners, examining the ability of groups to detect and respond adaptively to environmental gradients (Berdahl et al. 2013). The fish showed an enhanced ability to track preferred areas of habitat, in this case, patches of shade in a brightly lit environment, when in groups, and especially when in larger groups of 64 fish or more. Pigeons travelling in groups home more efficiently, compared to when they travel alone, reaching their destination more quickly and travelling by a more direct route (Dell'Ariccia et al. 2008). Sparrows presented with a novel foraging task performed better in larger groups of six birds than in pairs (Liker and Bokony 2009). The task of discriminating between potential nest sites by rock ants (*Temnothorax rugatulus*) fits the same pattern when the task is a complex one, to differentiate between two similar options, with groups outperforming individuals. However, when the task is simple, individuals solve the task better than groups (Sasaki et al. 2013). This finding demonstrates the advantage of swarm intelligence when animals are faced with challenging cognitive tasks, but also shows that when presented with a comparatively simple task, the potential costs of reliance on social information over personal information can derail the group decision-making process.

For most animals, decision accuracy has two facets: they must respond appropriately both to so-called true positives and to false positives. For example, prey animals need to be able to respond with evasive behaviour to a stimulus that indicates the approach of a predator (i.e. the stimulus is a true positive), while avoiding the costs associated with being excessively jittery and fleeing unnecessarily if the stimulus, such as a rustle in nearby bushes, does not in fact indicate the approach of a predator (i.e. the stimulus is a false positive). It is often considered that these two elements are linked – that a high degree of responsiveness to true positives inevitably connotes a proportionately high response to false positives; however,

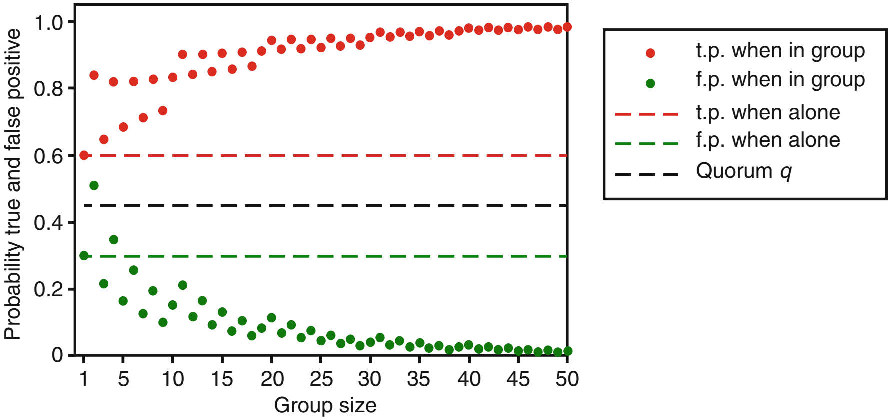

Fig. 8.7 Wolf and co-workers (2013) showed that at intermediate values of a quorum threshold, groups are able to simultaneously decrease their rate of false positives (*f.p.*) and increase their rate of true positives (*t.p.*) relative to solitary individuals (From Wolf et al. (2013))

mathematical models predict that animals in groups may be able to overcome this limitation using a quorum decision rule, enabling them to simultaneously increase true positives while decreasing false positives (Wolf et al. 2013; see Fig. 8.7).

8.6 Mechanisms Underlying Improvements in Decision-Making with Group Size

Having established that animal collectives are capable of implementing a solution to a problem that could not be achieved by a single group member, the question becomes: ‘how can this be done?’ When faced with uncertainty over the best course of action, animals need to obtain information in order to improve their decision-making, and social information gleaned from other group members is often the best solution. Broadly, there are two main mechanisms, either groups integrate and use the information of all members to arrive at some average of all preferences, or they identify those individuals with pertinent and accurate information and devolve the decision to these individuals. The underlying principle in the first of these instances is often referred to as ‘many wrongs’, as in the phrase ‘many wrongs make a right’. If each member of a group has some information, whether it be a guess as to the weight of an ox, or the best direction in which to travel, if this information can be pooled then the error in the overall group estimate will often be lower than the error of all, or almost all, individual group members. For this reason, it is suggested that animals in groups are often best served by decisions that include the contributions of a large number of group members. This contention was originally proposed in the context of bird migrations (Bergman and Donner 1964; Hamilton 1967; Wallraff 1978). If each bird independently has a preferred direction, but also has some error due to their interpretation of the available navigational cues, the flock in flight will tend to follow the mean of all its members' preferred directions because the individuals are constrained by their need for social cohesion. So long as the individual errors of the birds are scattered evenly about the correct travelling direction to a given destination, or in other words, there is no systematic bias that makes individuals mistakenly converge on a preference to one side of the correct direction, then the flock will accurately follow the correct route. Furthermore, since the standard error of the mean flying direction preference decreases with increasing flock size, larger flocks will tend to be more accurate in their approximation of what is the correct route (Rabøl and Noer 1973; Simons 2004).

But while the many wrongs principle, specifically the pooling of information and shared decision-making, provides a simple self-organised mechanism for the expression of swarm intelligence, its underlying assumptions may often be violated. For example, a key assumption of the wisdom of the crowd is that each individual should decide independently and that these independent decisions can then be integrated at the level of the group. However, social interactions and feedback often serve to shape the decisions of individuals, making this assumption potentially unrealistic for many decision-making contexts. Interestingly, as the earlier example of the collective deterioration in performance in some nest-site selection contexts shows, this feedback can actually prevent the true expression of the wisdom of the crowd (Sasaki et al. 2013). Furthermore, to be effective, the wisdom of the crowd is reliant upon a diversity of opinion among group members, which in turn relies on the independent sampling by group members of the available sensory information. If this information is highly correlated among individuals, as is often the case in complex environments, then this has the potential to introduce bias to their decision-making and actually to reduce the decision-making ability of larger groups, although this remains to be tested experimentally (Kao and Couzin 2014).

Alternative explanations to the wisdom of the crowd tend to emphasise the importance of well-informed individuals in shaping the group decision. Indeed, even among some of the classical examples of the wisdom of the crowd, it can be difficult to exclude the possibility that what appears to be a fully shared process is actually guided by a subset of the group assuming a dominant role in decision-making processes. It stands to reason that groups containing a larger number of individuals are proportionately more likely to contain individuals with better information. Larger groups are also more likely to have members with a more diverse range of skills and abilities. Assuming that individuals with the relevant experience, information and skills can influence the decision-making process, then larger groups will tend to make better decisions. Under this scenario, many of the group members will not contribute directly to the decision-making process, but can benefit from copying or scrounging the information (Guttal and Couzin 2010; Liker and Bokony 2009). Rather than applying the influence of all group members to find a solution, in these cases, groups are better served by allowing the best informed individuals to guide decision-making (Bisazza et al. 2014). This process does not necessarily require any complex cognition, nor recognition of who does, and who does not, have information. The study by Berdahl and co-workers (2013) demonstrated neatly how fish in groups are able to track environmental gradients efficiently, a feat that single individuals are incapable of. This is achieved simply through differences in the behaviour of individuals in response to local conditions, specifically that individuals in favoured areas of habitat tend to swim more slowly. The differences in speed across the group has the effect of causing the group to turn towards that area, while the slower speed of individuals already in the area produces an increase in local density and ultimately the group converges on that area. The larger the group, the greater the area that it covers and thus the more effectively it is able to detect and respond to the presence of environmental gradients at the collective level.

These two mechanisms – the wisdom of the crowd model and the leadership model – can coexist. Precise data obtained from pigeons fitted with GPS tracking devices suggests that pairs in flight can switch between a compromise approach approximating the wisdom of the crowd and leadership imposed by one member of the pair within the same flight (Biro et al. 2006). The switch between the two occurs once the level of conflict between an individual's fidelity to its chosen route and its social attraction to its flying partner increases above a threshold level. Below this threshold, the pigeons manifest the kind of averaging and compromise indicated by the wisdom of the crowds. Above the threshold, the compromise is broken with one individual assuming the role of leader and the other foregoing its own route preferences in order to retain its social bond, broadly as predicted by Couzin and coworkers' model described earlier (Couzin et al. 2005).

8.7 Summary

The outcomes of studies into collective decision-making in a wide variety of species demonstrate a remarkable ability of social animals to respond adaptively to a range of challenges, from selecting new nest sites to finding foraging patches and avoiding predators. A general pattern exists that animal groups are more effective at collecting, integrating and using information than single individuals. At the root of this ability are some fascinating yet often straightforward heuristics, such as the quorum responses highlighted in many animal taxa. But while we get to grips with the mechanisms of collective behaviour, further challenges remain. First, although empirical studies have largely and understandably focussed on the specific attributes of single model species, collecting data on a broader range of species would allow comparisons among related species and across different taxa. It would be fascinating to get to grips with the generalities of collective decision-making to identify potential cognitive, ecological and adaptive reasons for the similarities and indeed dissimilarities that exist so that we can appreciate the constraints, opportunities and evolutionary bases of this fascinating behaviour. Furthermore, and in addition to this point, we often examine snapshots of decision-making, whereas studies that operate over a longer timescale and ideally use free-ranging animals could provide not only greater understanding of the mechanistic side of this behaviour but also a much improved and much needed insight to the longer-term fitness consequences of a series of collective decisions over time. Second, a better understanding of collective decision-making goes hand in hand with understanding how animals communicate. For studies of collective motion and elements such as leadership, we often use the gambit of recording the order in which animals move. From this we infer the role played by individuals within the group decision-making process, yet this may represent an oversimplification in some instances, as exemplified by the movements of gorillas described earlier. Animals may communicate their preferences and intentions in many subtle ways before overt action is taken, and it behoves us to investigate this more thoroughly. Finally, incorporating heterogeneity into models and experiments of decision-making would allow us to understand both the relative influence of different individuals and the state dependence of leadership and potentially how animals of the same species execute collective decisions according to different circumstances and contexts within their lives.

Development, Ontogeny and Parasite-Mediated Changes in Social Behaviour

9

9.1 Introduction

Tinbergen (1963) identified the development of a behavioural trait during an animal's lifetime as one of the four key questions that should be asked about a given trait in order to understand it. The study of the development, or ontogeny, of sociality throughout animals' lives provides an insight to both the mechanisms of sociality and its functions. In this chapter, we examine first the development of sociality. Many animal species spend the initial stages of life in a social environment, for example, if eggs are clustered or young are born into a litter of sibs. This means that an aggregation of a cohort of kin is formed. These may subsequently go on to form a true social group, based on social attraction, or they may simply remain together through philopatry, and it can be difficult to distinguish between these. Nonetheless, the development of social attraction to conspecifics in early life has been examined in a few species in conjunction with the development of sensory and locomotive capabilities, and we describe these here. Once the ability to identify and locate conspecifics is developed, then the likelihood of an animal seeking out others of its kind in order to associate with them and to form groups is governed by a range of factors. These include the early-life social environment of offspring, the neural development of individuals, the action of hormones and the genetic predisposition of animals to sociality. We consider each of these in relation to the development and expression of sociality and further how this relates to the ecological context in which the animal operates. Following on from this, we consider how parasitism, a near ubiquitous reality for free-ranging animals, affects patterns of association among animals.

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9.2 Ontogeny of Sociality

While many animals exhibit sociality at some point during their lives, their social tendency is seldom expressed consistently throughout their lifetime, so we see ontogenetic changes as the animal grows and develops. Two main broad categories of animals are often proposed in respect of these ontogenetic changes, those that are gregarious as juveniles, but then become progressively more solitary as they age and reach adulthood, and, less commonly, those that are solitary as juveniles, but which tend to aggregate more as adults. In both cases, the reasons for these variations in social behaviour may rest in changes to the costs and benefits of aggregation according to the size or age of the animal.

9.2.1 Animals that Aggregate Mainly in Early Life

The aggregation of animals into social groups during their vulnerable early life stages is simple to understand from a functional perspective, given the considerable anti-predator benefits of sociality. Forming into groups decreases an individual's per capita risk and so increases that individual's fitness (Treisman 1975a, b). As animals grow, their risk of predation decreases, so they become less reliant upon grouping. At the same time, intraspecific competition for food or for territory increases, which can drive the break-up of groups as animals become solitary foragers or territory holders (Werner and Gilliam 1984). Many animals lay clutches of eggs, which predisposes the newly hatched young to form aggregations (Courtney 1984). Nonetheless, the aggregations can only be considered to be social if some degree of social attraction, however transient, exists between hatchlings. In many cases, the strength of this social attraction decreases over time, and the animals become progressively more solitary. This pattern is exemplified by social caterpillars, which are strongly social during their earliest life stages, but become progressively less so as they grow (Costa et al. 2003; Fitzgerald 1993). Forest tent caterpillars (*Malacosoma disstria*; see Fig. 9.1) are attracted to conspecific chemical cues during their first larval instars. The animals produce and follow silk trails that are laden with pheromone, which act to maintain group cohesion. As they develop further, however, they become less reliant on the silk trails and show increased independence in their movement and foraging behaviour (Despland and Hamzeh 2004). The underlying mechanism for this change is likely to be an age-related change in their neural responses to stimuli that act to decrease their inhibition to move independently. A broadly similar pattern is seen in many spider species, the majority of which hatch en masse from egg sacs and spend a short period of time at the beginning of their lives in a gregarious phase. A study of the solitary spider, *Agelena labyrinthica*, which forms such aggregations following hatching demonstrated how the tendency to aggregate decreased gradually over the first 6 weeks of life. A simple set of interaction rules describe this process. Spiderlings were initially more likely to decrease activity in the presence of conspecifics, resulting in the maintenance of groups, but their activity in the presence of conspecifics increased over time leading to the dispersal of the groups (Mougenot et al. 2012).

Fig. 9.1 An aggregation of tent caterpillars (Photo J.R. Carmichael)

Mammals and birds enjoy a period of parental provisioning in early life; however, even once this is complete, the juveniles may remain with their parents and siblings, or an extended social group, up to sexual maturity and beyond. Young mammals begin to exercise a degree of independence from their mothers over time, interacting with other newborns. When given a choice between associating with their mother and associating with another youngster, both lambs and calves elected to join their mothers prior to weaning, but reversed this choice after weaning (Veissier et al. 1990; Walser et al. 1983). Interactions with peers can be extremely important in developing long-term social bonds that may last for the lifetimes of those animals. For example, goat kids form into cohesive peer groups with both their sibs and with unrelated juveniles by the end of their second week (Lickliter 1987). Similarly, in another ungulate, Przewalski's horse (*Equus ferus przewalskii*) foals begin to leave their mother's side to interact extensively with other foals at the age of just 3 weeks (Boyd 1988). This pattern exists across most equid species, although the interactions between the foals differ between the sexes with greater aggression in the play of male foals than females, foreshadowing the agonistic behaviour that will form an important part of their repertoire after maturity (Carson and Woodgush 1983). Whether this so-called play fighting is a direct precursor to adult aggression is a matter of contention with some authorities considering it to be distinct and as having different functions, while others stress the similarities between juveniles play fighting and adult fighting both in terms of the neurological bases and behavioural expression (Delville et al. 2003; Pellis and Pellis 1988, 1998).

The pattern and frequency of social interactions shown by younger mammals tend to change as they develop and eventually reach adulthood. This may be measured in terms of social distance, simply the distance measured between animals, which tends to increase over their lifetimes. For example, young eland (*Taurotragus oryx*) show social distances of less than 1 m to their peers in very early life. This increases up to 4.5 m in later in their juvenile stage and up to 11 m in adults (Hillman 1974, 1979). In many mammal societies, one sex, usually the male, will leave the natal group, either leave of their own accord or because they are driven out by resident males, to whom they now represent a competitive threat. By contrast, in many cases female offspring remain with their natal group. So while females in such groups tend to be social throughout their lives, males may only be social as juveniles, although in some instances, for example, in cheetahs (*Acinonyx jubatus*) and some dolphin species, males form into bachelor groups.

Among social bird species, juveniles tend to form larger flocks than adults, a pattern that has been recorded in a diverse range of bird taxa, including corvids (Delestrade 1994), passerines (Catterall et al. 1989), galliforms (Kruijt 1964) and ratites (Bertram 1992). Moreover, as with mammals, social distance increases with age in many species. In ostriches (*Struthio camelus*), juveniles are highly gregarious and maintain cohesive groups of up to 25 individuals, whereas adults are often solitary outside the breeding season (Bertram 1992). In the Burmese red jungle fowl (*Gallus gallus spadiceus*), chicks show strong social attraction to other chicks and aggregate into tight groups from their second day following hatching. These groups gradually become less cohesive as the birds develop (Kruijt 1964).

By maintaining close contact with peers, juvenile birds and mammals gain a degree of protection from threats, potentially including aggression from older, dominant conspecifics. In addition, their lack of experience means that these associations provide an opportunity to obtain the benefits of social learning and to form alliances that will shape their future interactions within the social group. These benefits decrease over time as the juveniles become more experienced and progressively better able to deal with threats. At the same time, aggression tends to increase as the animals develop; dominance hierarchies develop, and individuals, particularly males, begin to compete for mating opportunities. This aggression is inimical to the maintenance of cohesive groups, so the animals tend to increase the spacing between themselves and others.

In most, but not all cases, the changes in social behaviour and increases in aggression are driven by hormonal changes in the animals (see Trainor et al. (2009) for a detailed consideration of this topic). For example, oxytocin and oxytocin-like hormones are known to be extremely important in the manifestation of social behaviour and social preferences in vertebrates. Mesotocin, the avian homolog of oxytocin, increases the tendency of zebra finches (*Taeniopygia guttata*) in particular to associate with large groups and with familiars, particularly in female birds (Goodson et al. 2009). In addition, increased aggression, often linked to hormonal changes, can drive groups apart. The onset of fighting behaviour between jungle fowl chicks at the age of 3 weeks coincides with increases in plasma testosterone in males at that same age (Kruijt 1964; Tanabe et al. 1979). Gonadal hormones are known to regulate aggression between males of many species, especially during the breeding season (Nelson 2000; Sinervo et al. 2000). Furthermore, competition between males causes short-term increases in testosterone and elevates aggression as a consequence (Wingfield et al. 1987, 1990). Outside the breeding season, aggression between males is controlled by the conversion of testosterone, or its precursor dehydroepiandrosterone (DHEA), to oestrogen (Soma and Wingfield 2001; Wingfield et al. 2001). However, the effects of specific hormones and neuropeptides on aggression can vary

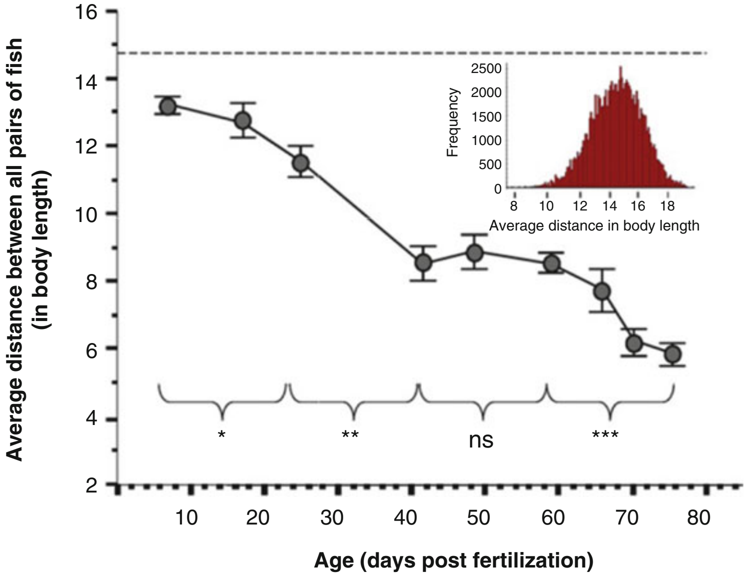

Fig. 9.2 Buske and Gerlai (2011) examined the development of social attraction in zebrafish. The average (±SE) distance in body lengths between pairs of zebrafish as a function of time during early life. The inset box shows the interindividual distances in body lengths that would be expected given a random distribution of fish within the tank. The peak value of this simulation is shown as a dashed line. Comparisons between the interindividual distances of fish at different ages were made using repeated-measured ANOVAs: *ns* = not significant, $* < 0.05$, $** < pb\ 0.01$, $*** < 0.001$ (From Buske and Gerlai 2011)

between and even within species. Neuropeptides, in particular arginine vasopressin and serotonin, act to inhibit aggression in some species, but may actually promote aggression in others (Goodson 1998a, b; Goodson and Adkins-Regan 1999; Edwards and Kravitz 1997; Sperry and Wingfield 2003; Ten Eyck 2008). Testosterone has a different effect in females and may actually decrease aggression (Elekonich and Wingfield 2000). Behavioural endocrinology has provided some fascinating insight to the mechanisms behind the expression of social behaviour, particularly in birds (Anacker and Beery 2013; Carter et al. 2008; Chapman 1990), and this promises to be an extremely fruitful area for future research in a broad range of taxa.

Many aquatic vertebrates are often described as being either social throughout their lives or as being social as juveniles and solitary as adults. In fact, the reality is rather more complicated than this as many species are not gregarious in the first few days or weeks of life and only begin to show social attraction to conspecifics later in their development. Zebrafish (*Danio rerio*) become progressively more social over the first few days and weeks of their lives. While week-old fish tend to maintain a distance of over ten body lengths to conspecifics, this gradually decreases over time so that 10-week-old fish are separated by around six body lengths (Buske and Gerlai 2011; see Fig. 9.2). The increase in shoal cohesion in these fish is accompanied by changes in the neurobiology of the fish, specifically in relation to changes in the levels of dopamine, serotonin and other candidate neurotransmitters (Beckers et al. 1993; Seeley and Towne 1992).

Tadpoles of the common frog (*Rana temporaria*) only aggregate in the middle and later stages of larval development (Nicieza 1999). Tadpoles are highly vulnerable to predators, especially as they metamorphose into their adult form. It has been suggested that aggregation during larval development may serve to promote synchrony in metamorphosis as the simultaneous emergence of large numbers of juvenile frogs may be an adaptation to swamp the short-term capacity of predators to consume them (Arnold and Wassersug 1978; Devito et al. 1998; Ims 1990). Beyond this stage, almost all adult anurans are nonsocial. Similarly, social fish species are not typically attracted to conspecifics following hatching, but only begin to form aggregations following metamorphosis (Fuiman and Magurran 1994). This may imply a survival advantage to dispersion in larval fish; given their relatively weak motor skills, it may be advantageous to be solitary in order to forage and avoid predators at this stage in development. Alternatively, the lack of any tendency to aggregate may reflect a constraint in their ability to form groups. Shoaling behaviour in striped jack (*Pseudocaranx dentex*) only begins once individuals attain a size of around 12 mm, when they develop the sensory apparatus necessary to perceive conspecifics and the motor skills required to respond appropriately to them (Masuda and Tsukamoto 1999).

9.2.2 Animals that Aggregate Mainly in Later Life

The pattern whereby animals begin life being solitary before becoming progressively more social is much rarer than the reverse. Those species that are solitary in early life often rely on crypsis or camouflage during this stage of their lives. One of the best studied examples of this strategy is provided by the New Zealand rock lobster (*Jasus edwardsii*). Butler and co-workers (1999) tested the attraction of these lobsters to shelters that were associated with conspecific chemical cues versus and to shelters in the absence of such cues. Juveniles showed no preference for shelters presented with conspecific cues. In fact, their response to conspecific chemical cues appeared to be neutral or possibly even repulsive whereas subadults were strongly attracted to such shelters. Moreover, the study demonstrated that the juveniles had greater survivorship when living solitarily, whereas the subadults garnered the greatest benefit by living in groups, as this enables them to defend themselves collectively against attackers. The Caribbean spiny lobster (*Panulirus argus*) shows a similar ontogenetic transition from a solitary to a social existence (Childress and Herrnkind 1996). During their earliest postlarval stages, the lobsters gain the shelter provided by algal beds and are solitary and unresponsive to the presence of conspecifics. As they develop, the lobsters leave the algal beds and congregate into shelters with conspecifics. This social attraction is also mediated by conspecific chemical cues (Ratchford and Eggleston 1998). Unlike the New Zealand spiny lobsters, however, the Caribbean species appears to gain no benefit through cooperative defence, nor do they appear to benefit from grouping through simple dilution effects. Instead, their attraction to conspecific cues appears to function to allow them to home in on crevices that provide them with refuge. The response to conspecific cues in this species therefore seems to simply be a means to locating a scarce but essential resource, rather than being social attraction in its purest sense, although as the authors conclude, this might be an evolutionary step towards more complex social behaviour (Childress and Herrnkind 2001).

Another crustacean that forms social aggregations, albeit on a much larger scale, also spends the early stages of its life being solitary before later becoming social. Antarctic krill (*Euphausia superba*) only start to form aggregations once they reach a size of approximately 10 mm (Hamner et al. 1989). The reason for this ontogenetic shift in behaviour is not well understood, but krill are thought to aggregate in order to avoid predators, to find food or mates and to obtain hydrodynamic advantages (Hamner and Hamner 2000; O'Brien 1987; Ritz et al. 2011). In addition to these general benefits, Ritz (2000) suggests that as the energy required to resist sinking increases with mass, one of the reasons that Antarctic krill above 10 mm in size join social aggregations is to exploit the upwellings created by groups of conspecifics to offset these costs.

9.3 Effects of the Rearing Environment on the Development of Sociality

The social behaviour of animals is influenced by the conditions they experience in early life and, before this, by the conditions experienced by their mothers. In the case of these maternal effects, the condition of the mother and the social environment in which she exists influences the development of the foetus, most probably through the expression of maternal hormones (Sachser and Kaiser 2010). This can have profound effects on the behaviour of offspring. For example, female three-spined sticklebacks that have been exposed to predator stimulus produce eggs with higher concentrations of egg cortisol. The resulting offspring exhibit smaller nearest neighbour distances and, consequently, tighter shoaling behaviour than the offspring of mothers that were not exposed to predator stimulus (Giesing et al. 2011). Following birth, or hatching, interactions with conspecifics play a crucial role in shaping patterns of social behaviour.

Juvenile mammals often actively seek out and initiate social interactions (Fairbanks 1993; Pusey 1983). In doing so, they may increase their level of social competence and ultimately their fitness, if their ability to manage social relationships translates to increased future reproductive success (Byrne and Whiten 1988). Early social experiences may be especially important among species that live in social groups. A comparison across three South American species of canids revealed that pups of the bush dog (*Speothos venaticus*), which usually lives in small packs, engaged longer in play than pups of the maned wolf (*Chrysocyon brachyurus*), a largely solitary species, or pups of the crab-eating fox (*Cerdocyon thous*), which typically lives and hunts in pairs. Interestingly the complexity of the play did not relate to differences in the degree of sociality between the species and may instead be determined by the development of foraging skills through play (Kleiman 2011).

Early social experience is now known to affect not only the patterns of behaviour expressed by animals in later life but also the architecture of the brain itself. Where animals are reared in social isolation, this can often quite dramatically impair the development and later expression of social behaviour (Lukkes et al. 2009). In particular, individuals reared in isolation may show reduced cognitive development, abnormal responses to stressors and poor decision-making (Baarendse et al. 2013; Einon and Morgan 1977; Fone and Porkess 2008). By contrast, animals reared in social environments tend to show greater social competence, exemplified by the development of appropriate responses to social interactions in later life (Arnold and Taborsky 2010; Taborsky and Oliveira 2012). Neurological development is known to be sensitive to early life experience, both in terms of the structural development of the brain itself and in terms of the development of neuroendocrine systems such as the hypothalamic-pituitary-adrenal hormonal axis, which controls the response to stress, among other things, in mammals and birds. In zebra finches, nestlings that experience high levels of competition with siblings tend to show correspondingly increased levels of stress hormones, such as corticosterone. Boogert and colleagues examined the effect of elevated corticosterone in chicks on their patterns of social behaviour in later life. They found that such animals tended to increase the number of flock mates that they associate with and made them less choosy about who they associated with (Boogert et al. 2014). Early social stimulation can produce changes in the development of specific areas of the brain, for example, common frog (*Rana temporaria*) tadpoles reared at high density developed larger optic tecta (the part of the brain involved in the processing of visual information) (Trokovic et al. 2011). Similarly, ninespine sticklebacks reared in groups developed larger optic tecta but smaller olfactory bulbs than individually reared fish, which likely reflects plasticity in neural development, shaped by the availability of different sensory cues in this case (Gonda et al. 2009). Fischer and co-workers reared cichlid fish (*Neolamprologus pulcher*) under different social treatments and found that although overall brain size was not greater in the fish reared in large groups, the relative size of certain parts of the brain, including the hypothalamus and the cerebellum, was greater (Fischer et al. 2015). The increase in the size of the hypothalamus is particularly interesting, since this brain region is strongly implicated in the control of social behaviour. Broadly speaking, social stimulation during early life seems to increase the size of brain regions or of the brain as a whole (Adar et al. 2008; Fowler et al. 2002; Lipkind et al. 2002; Ott and Rogers 2010; see also Gonda et al. 2009). This developmental pattern parallels the broader hypothesised evolutionary relationship between brain size of primates and their social complexity (Dunbar 1998; Dunbar and Shultz 2007) and the correlation between relative brain size and sociality in other mammal orders (Perez-Barberia et al. 2007) (see also Chap. 10).

Social stimulus may be provided by parents, or by peers, or by the broader social milieu. Early social interactions play an important role in shaping the choice of social partners in later life. The availability of several zebrafish (*Danio rerio*) colour morphs enabled Engeszer and co-workers to investigate environmental effects on the development of shoaling preferences. Fish preferred to associate with individuals that had the same pigment pattern strain as those they had been reared with, even if that pattern was different to their own, demonstrating a clear ontogenetic learned effect on social preferences (Engeszer et al. 2004). Furthermore, once established, these association preferences remained consistent throughout the lives of the fish. Warburton and Lees earlier examined the social behaviour of fish raised with heterospecifics and found that these fish retained a preference to associate with heterospecifics over conspecifics in shoals (Kozak and Boughman 2008; Warburton and Lees 1996). Early experience can also have profound effects on the likelihood of an animal showing species-typical patterns of social behaviour in later life. Orphaned juvenile chimpanzees showed different patterns of social development to those reared by their mothers, including being more aggressive (van Leeuwen et al. 2014). For the majority of species which do not engage in parental care, early social interactions encompass a variety of conspecifics and potentially also heterospecifics. The tactile cues provided by aggregated conspecifics stimulate and accelerate the development of cockroach (*Blattella germanica*) nymphs (Holbrook et al. 2000; Lihoreau and Rivault 2008; Roth and Willis 1960). Conversely, larvae of common frogs raised in isolation grew more quickly than those raised in groups, although the group-raised individuals were more than twice as active as their isolated peers (Nicieza 1999). These results may reflect, respectively, the competition experienced by group-living animals and the adoption of different antipredator strategies according to rearing conditions – crypsis for solitary animals versus risk dilution and other group-related defences for gregarious animals.

9.4 Ecological and Environmental Effects on the Expression of Social Behaviour

Animals base many of their group-joining, or group-leaving, decisions on their estimation of the level of threat or on the distribution of resources, including food and shelter. These decisions represent flexible and strategic adaptation to what are often localised and short-term contexts, and we consider some of these in Chaps. 7 and 8. But the social tendency of an animal can change over the longer term and often for reasons outside the animal's direct control. We consider three examples of ecological and environmental factors that interact with social behaviour: induced effects, which produce dramatic changes in behaviour in a small number of species, the effect of pollutants and the effect of infection by parasites.

9.4.1 Induced Effects

Changes in behaviour in response to the local density of conspecifics are predicted by models and have been observed in animal groups (Buhl et al. 2006; Vicsek et al. 1995). In particular, as density increases, individuals self-organise into

Fig. 9.3 Solitary and gregarious forms of the desert locust (*Schistocerca gregaria*). The scale bar represents 2 cm (From Simpson et al. 1999)

structured, polarised groups, and we examine this and related phenomena in Chap. 3. Some locust species undergo a dramatic change in morphology and behaviour in response to increases in density. Desert locusts (*Schistocerca gregaria*) exist in two clearly distinguishable forms – a green-coloured morph, which is solitary, and a yellow and black, highly gregarious morph (see Fig. 9.3). The locusts switch from the solitary form to the gregarious form when the local population density increases and conditions become crowded. The key sensory mechanism behind this transition is the tactile stimulus provided by collisions that occur in large numbers of conspecifics (Simpson et al. 1999). Stimulation provided by these tactile cues triggers a cascade of physiological and hormonal changes within the locust. Behaviourally the animal begins to transform from a solitary animal to a gregarious one over just a few hours. In addition, the animal changes in colour, taking on a yellow and black aposematic colouration, which reflects a switch to a diet including toxic plants (Sword et al. 2000). Maternal effects are expressed as female locusts in the gregarious phase pass on these behavioural characteristics to their offspring (Maeno and Tanaka 2010; McCaffery et al. 1998; Tanaka and Maeno 2010).

9.4.2 Anthropogenic Impacts on Social Behaviour

In Chap. 2, we discussed how social attraction and social organisation are founded on the ability of animals to recognise one another. Anthropogenic activities are known to interfere with animal communication and social recognition (Lurling and Scheffer 2007; Rohwer and Ewald 1981). This so-called info-disruption can be induced both by direct contamination of the environment and by factors such as climate change, ocean acidification and increasing levels of carbon dioxide in the atmosphere (Roskaft et al. 1986). Contaminants can affect communication either by changing the chemical signature of an organism, by interacting with the chemical information that is transferred between individuals, by damaging the chemosensory

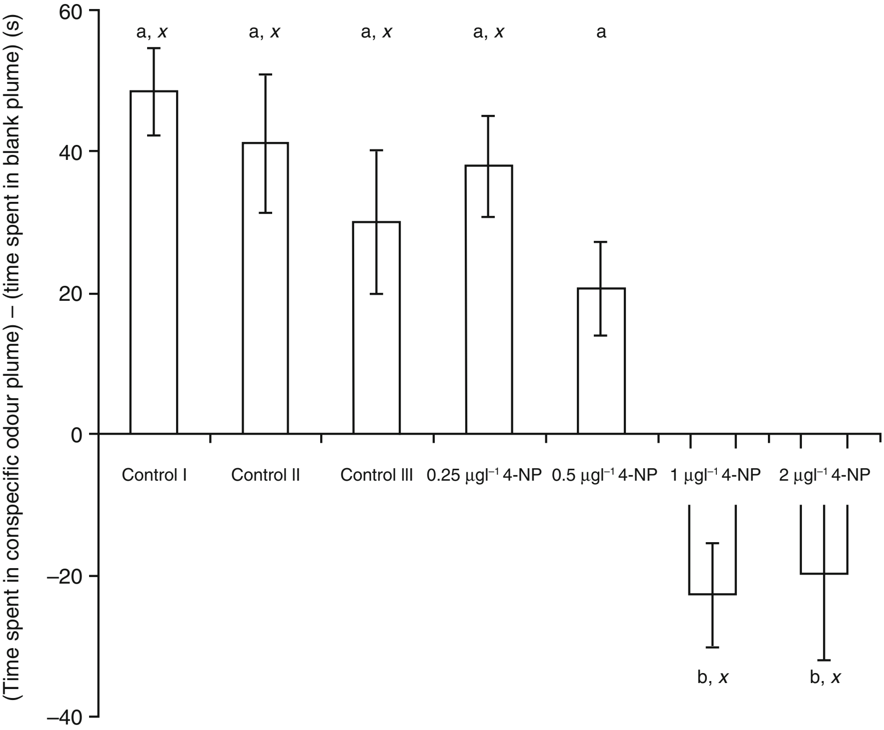

Fig. 9.4 Ward and co-workers examined the response of banded killifish to conspecific cues in a flume. In control treatments, and at low doses of the contaminant, 4-nonylphenol (4-NP), fish preferred to occupy a chemical plume containing conspecific chemical cues. At higher doses of 4-NP, the fish avoided conspecific cues, which could have implications for the social organisation of the fish. The letter, *x*, represents a deviation from the null expectation of no difference in time spent in the conspecific plume versus time spent in the blank plume. Letters *a* and *b* represent subgroups identified by post hoc testing (From Ward et al. 2008a)

abilities of an organism or by a combination of these. While many studies have documented the effects of various chemicals on chemical communication, most have been concerned with the effect of info-disruptors on foraging, reproductive behaviour or on predator-prey interactions; relatively few have related this directly to sociality. Of those that have, most have concerned the effect of contaminants on social behaviour in aquatic animals. For example, low doses of the chemical nonylphenol, even following short-duration exposures, caused banded killifish (*Fundulus diaphanus*) to orient away from the chemical cues of conspecifics (Ward et al. 2008a; see Fig. 9.4). Similarly, choice tests performed using a related species, the mummichog (*Fundulus heteroclitus*), following exposure to benzyl butyl phthalate demonstrated the breakdown of normal social association patterns (Hogstad 1987). Clearly, far more work needs to be done in this area, both on aquatic and on terrestrial organisms. As well as providing valuable information to help us understand and hopefully mitigate the pernicious effects of some contaminants, such studies can shed light on the mechanisms of recognition.

9.4.3 The Effect of Parasites on the Expression of Social Behaviour

The behaviour of animals can be influenced, sometimes dramatically, by parasites. The changes in behaviour may reflect an adaptive response to avoid being parasitised in the first place, or they may be a consequence of having already been parasitised. These two contexts, which we might refer to as pre-infection and post-infection behavioural changes, are both known to affect the costs and benefits of group membership for host animals (see Chap. 4) which in turn shapes the social behaviour of potential hosts as they seek to mitigate the risks and costs of parasitism. Arguably pre-infection studies have been primarily focussed on host responses to ectoparasites, while post-infection studies achieve a better balance between the effects of ecto- and endoparasites.

In addition to this, researchers have considered the adaptive benefit of sociality in reference to its consequences for parasitic infection of group members. In general, we can differentiate between two main categories of parasites according to the manner in which they are transmitted: those that are directly transmitted through contact with, or at least close proximity to, infected conspecifics and those that are not transmitted through contact but which locate and parasitise their hosts by other means. In the first case, an individual's risk of parasitism should increase with group size, as greater densities of conspecifics increase the frequency of interactions overall and hence provide parasites with more chance to move between hosts. In the second case, it is predicted that an individual's risk of parasitism decreases with group size through the encounter-dilution effect (Mooring and Hart 1992). In fact, a meta-analysis performed by Rifkin et al. (2012) found a weak, positive relationship between group size and the risk of parasitism, regardless of the method of transmission, across a range of host and parasite species (see also Cote and Poulin 1995). Nonetheless, there are examples where host animals adjust their behaviour to counteract the risk posed by mobile, searching parasites, such as mosquitoes and other parasitic flies. In many cases, this involves the host animals forming larger groups, thereby diluting each individual host's risk of parasitism. For example, black grouse (*Tetrao tetrix*) form larger groups in the summer months, during which they are harassed by black flies (Simuliidae) (Ratti et al. 2006). A more extensively researched example is provided by herds of reindeer and their behaviour in response to the emergence over the summer months of warble flies and bot flies, which seek the herds out and exact considerable costs (Anderson and Nilssen 1996a, b; Helle 1980; Helle et al. 1992; Skogland 1989). By forming large aggregations, females and juveniles in particular appear to gain respite from the attentions of these insects; moreover, the low density of predators seems to rule out antipredator behaviour as a competing hypothesis for the formation of herds (Fauchald et al. 2007). Similarly, larger groups of horses appear to suffer lower per capita effects of parasitism by mosquitoes (Cozzie and Irby 2010), suggesting that an increased tendency to aggregate may be an effective means of limiting the effects of mobile, searching parasites. In addition, animals in groups may be better able to acquire social information about areas of their habitat associated with high parasite activity and to use this information to avoid such areas. Rainbow trout in groups were better able to avoid areas of their habitat infested with high levels of eye fluke (*Diplostomum pseudospathaceum*) cercariae and consequently were less likely to be infected (Karvonen et al. 2004). In some contexts, therefore, sociality may represent an adaptive response to elevated risk of parasitism, especially to the risk posed by highly mobile ectoparasites; however, more research needs to be done to study its effectiveness in mitigating the risks of infection by endoparasites in particular.

Once infected with a parasite, how does the social behaviour of the host change? In many cases, infection can bring about changes in host behaviour through direct manipulation by the parasite or simply as a by-product of infection. Parasites may manipulate their hosts in order to increase their chances of transmission to a subsequent host. They achieve this by targeting host systems, in particular the nervous and endocrine systems (Lafferty and Shaw 2013). Alternatively, the parasite may trigger an immune response in the host, which can be expressed as sickness. In both cases, although the mechanisms differ, infection by a parasite can alter the expression of social behaviour in the host. Banded killifish (*Fundulus diaphanus*) infected with a digenean trematode, *Crassiphiala bulboglossa*, are less likely to be found in shoals, either because the parasite reduces their swimming ability, leaving infected hosts less able to maintain social contact with conspecifics, or because the energetic costs that it exacts mean that the host has to spend relatively more time foraging, and this change to the host's activity patterns effectively leads to its isolation (Conradt and Roper 2000; Krause and Godin 1994; Ward et al. 2002b). Beyond these simple by-products of infection, however, both Krause and Godin and Ward et al. noted that infected fish were more likely to be found in peripheral positions when they were found in shoals. Both being isolated and being in peripheral positions potentially increase the risk of being predated by the parasite's final host, which may suggest that the effects on their host are adaptive for the parasite. Similarly, the eye fluke (*D. spathaceum*) damages the eyesight of its fish host and, in doing so, reduces their ability to shoal with conspecifics, which increases their risk of predation by the fluke's final avian host (Seppala et al. 2008). When amphipods (*Gammarus pseudolimnaeus*) detect the chemical cues of their predator, the brook stickleback (*Culaea inconstans*), they form into aggregations, which reduce their per capita risk of predation. However, amphipods infected with the acanthocephalan parasite (*Corynosoma* sp.) do not aggregate and so are more likely to be eaten by the predator, in turn infecting the stickleback (Lewis et al. 2012; see Fig. 9.5). In the above cases, it is difficult to prove beyond doubt that this amounts to adaptive manipulation by the parasite in its strictest sense, partly because the effects of parasitism may render infected animals more vulnerable to all predators and not only the final host, so the fitness benefit to the parasite is not conclusively demonstrated (Poulin 2010).

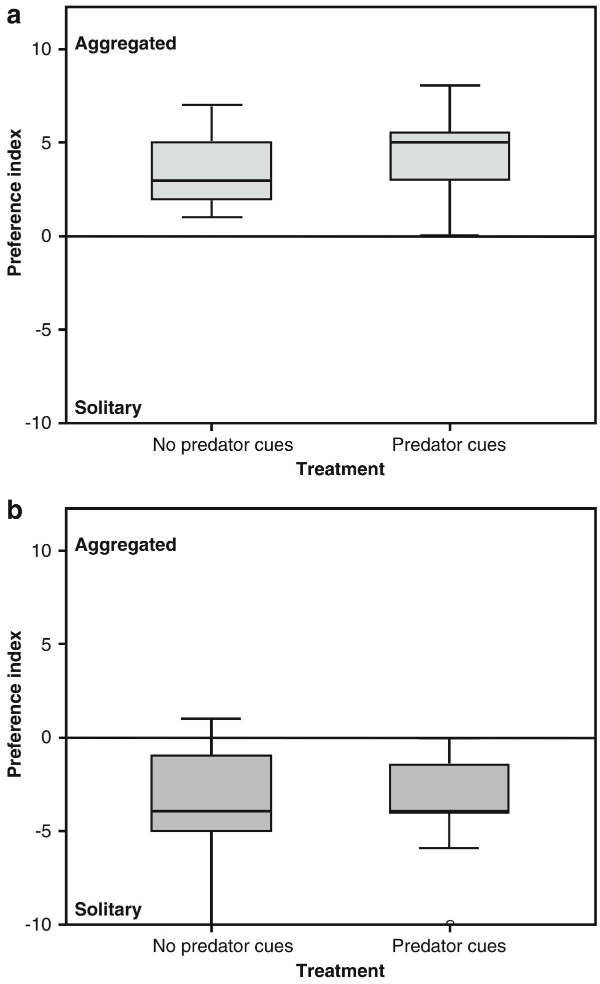

Fig 9.5 Lewis and co-workers (2012) constructed a preference index for amphipods, *Gammarus pseudolimnaeus*, that (**a**) showed no signs of infection with an acanthocephalan parasite, *Corynosoma* sp., and (**b**) that were infected with the parasite. Unparasitised amphipods were more likely to aggregate relative to parasitised conspecifics (From Lewis et al. 2012)

Whereas some parasites cause a reduction in the tendency of the host to aggregate, others produce the opposite effect. The strepsipteran parasite, *Xenos vesparum*, induces a series of changes in the behaviour of its paper wasp host (*Polistes dominulus*) including making them more gregarious. Following infection, the wasp ceases to contribute to normal tasks within its colony and eventually leaves the colony altogether to form into an aggregation with other parasitised wasps. The function of these wasp aggregations appears to be to allow the parasites to mate. Following this, those hosts that are infected with male parasites die, while those infected by females overwinter in the aggregation. The infected wasps remain in this aggregation long after healthy wasps have departed to found new colonies in the spring, only leaving when these colonies have begun to become established and to produce new workers. At this stage, the parasite can use its host to disperse its offspring to the new cohort of wasps (Beani et al. 2011; Hughes et al. 2004). Parasitic infection also causes an increase in the swarming behaviour of two aquatic crustacean species, *Artemia franciscana* and *Artemia parthenogenetica*. Interestingly, this effect can by produced by different species of parasite, by a cestode, *Flamingolepis liguloides*, and by microsporidians, *Anostracospora rigaudi* and *Enterocytospora artemiae*. The swarming behaviour, coupled with an increase in the intensity of the colouration of infected *Artemia* and an increase in surfacing, increases their conspicuousness to filter feeding birds, in particular the greater flamingo, which is the final host of the cestode. The changes in host behaviour caused by the microsporidians increases the efficiency with which the parasite can directly infect new *Artemia* hosts (Rode et al. 2013).

In addition to the effects of parasitic infection on the host organism, the behaviour of potential group members towards that individual may change, particularly if the parasite in question is capable of horizontal transmission and is contagious. Avoidance of infected conspecifics allows a simple, adaptive means of reducing the risk of parasitic infection. In binary-choice tests, fish are known to avoid conspecifics that appear to be parasitised, even if their appearance has been manipulated and the stimulus animals are not in fact carrying a parasite (Krause and Godin 1996b). Three-spined sticklebacks are known to avoid conspecifics carrying the fish louse, *Argulus canadensis* (Dugatkin et al. 1994). Interestingly, however, the fish show no obvious avoidance behaviour to the louse itself, suggesting that the cues that the fish respond to are derived from the coupling of the louse with an infected stickleback and so may be chemical cues relating to the damage caused by an attached louse. In fact, the identification of conspecifics that are infected by parasites is very often mediated by chemical cues, not only because chemical cues provide the most broadly used means of social recognition in many species, and in many cases are affected by host immune responses that act to communicate the presence of a parasite, but also because in the case of ectoparasite infection, visual cues may be scant or non-existent (Kavaliers et al. 2004, 2005). Caribbean spiny lobsters avoid shelters occupied by conspecifics infected by a virus, preferring to shelter alone rather than in the presence of such a conspecific even in the presence of a predator (Behringer and Butler 2010). Chemical cues are of primary importance in the social recognition of lobsters, and it is likely that infection with the virus affects the chemical cues given off by infected individuals.

9.5 Summary

Of the four questions highlighted by Tinbergen, the study of the ontogeny of social behaviour is arguably the most neglected. The development of social recognition and aggregation in early life has been well studied in a few species of larval and juvenile fishes, providing a fascinating picture of the relationship of this to the development of neural and locomotor performance. Yet there are many other taxa for which this information is scant or missing. Few organisms show consistent patterns of social organisation throughout their lives, and most of those that do are social as juveniles, but much less so as adults. The typical reason for this pattern is that adult animals, usually being larger, benefit from a reduction in predation risk. Additionally, the imperative to reproduce may often result in a reduction in the drive to affiliate with large numbers of conspecifics. Even among species that are social only for part of their lives, the environment that they experience in early life can have profound effects on their social behaviour subsequently. This is particularly important for the formation of an individual's repertoire of social behaviour patterns, such as the establishment of social association tendencies and preferences. Fascinating insight has been provided by studies that have integrated behaviour with physiology and endocrinology in this respect, and this remains a promising and likely a fruitful field of research. In addition to purely intrinsic, ontogenetic factors, the expression of social behaviour by an animal is often influenced by factors such as parasitism. Where infection results in a reduction in social behaviour, it may be difficult to resolve whether this is the result of active avoidance of the infected individual by potential group mates or the pathology of the infection, simply from observation; hence, experiments need to be designed carefully to separate these confounds.

The Evolution of Group Living

10

10.1 Introduction

When and how did group living evolve? Direct evidence of ancient animals living in groups is hard to come by, and adage has it that behaviour does not fossilise. In fact this is not strictly true, and some paleontological remains have been seen as providing evidence of animals living in groups, albeit with varying degrees of controversy. The abundance of remains of Pleistocene carnivores such as the dire wolf (*Canis dirus*) and Smilodon (*Smilodon fatalis*) found in the La Brea Tar Pits in California, viewed in conjunction with what we know of the scavenging behaviour of contemporary social carnivores, has led to some researchers to speculate that these species too were social (Carbone et al. 2009; Van Valkenburgh et al. 2009). Far earlier still, the Cretaceous-era trackways left by dozens of small theropod dinosaurs and a single larger animal in what is now Lark Quarry in Queensland, Australia, have been suggested by some workers to provide evidence of a stampeding herd, fleeing the approach of a predator (Thulborn and Wade 1979, Fig. 10.1). This interpretation has stirred debate, and more recent analyses conclude that the large dinosaur is most likely an herbivore and that the tracks attributed to the herd of smaller dinosaurs may actually have been laid down sequentially over a longer period of time as individuals forded a shallow or partially dried river crossing (Romilio and Salisbury 2011). While acknowledging the difficulty of inferring sociality from paleontological evidence, we can nevertheless speculate about group living in long extinct species. It is likely that animals living in past environments faced the same kinds of challenges as do contemporary ones, such as finding food, avoiding predators, effectively navigating and so on, and it is not unreasonable to imagine that they met these challenges in many of the same ways, including by forming groups. This speculation is further bolstered by the observations that a diverse range of extant species spend at least some portions of their lives in groups and that among these lineages group living appears to have evolved multiple times, suggesting that group formation might be a common evolutionary response to particular selection pressures. Phylogenetic analysis allows researchers to map patterns of grouping

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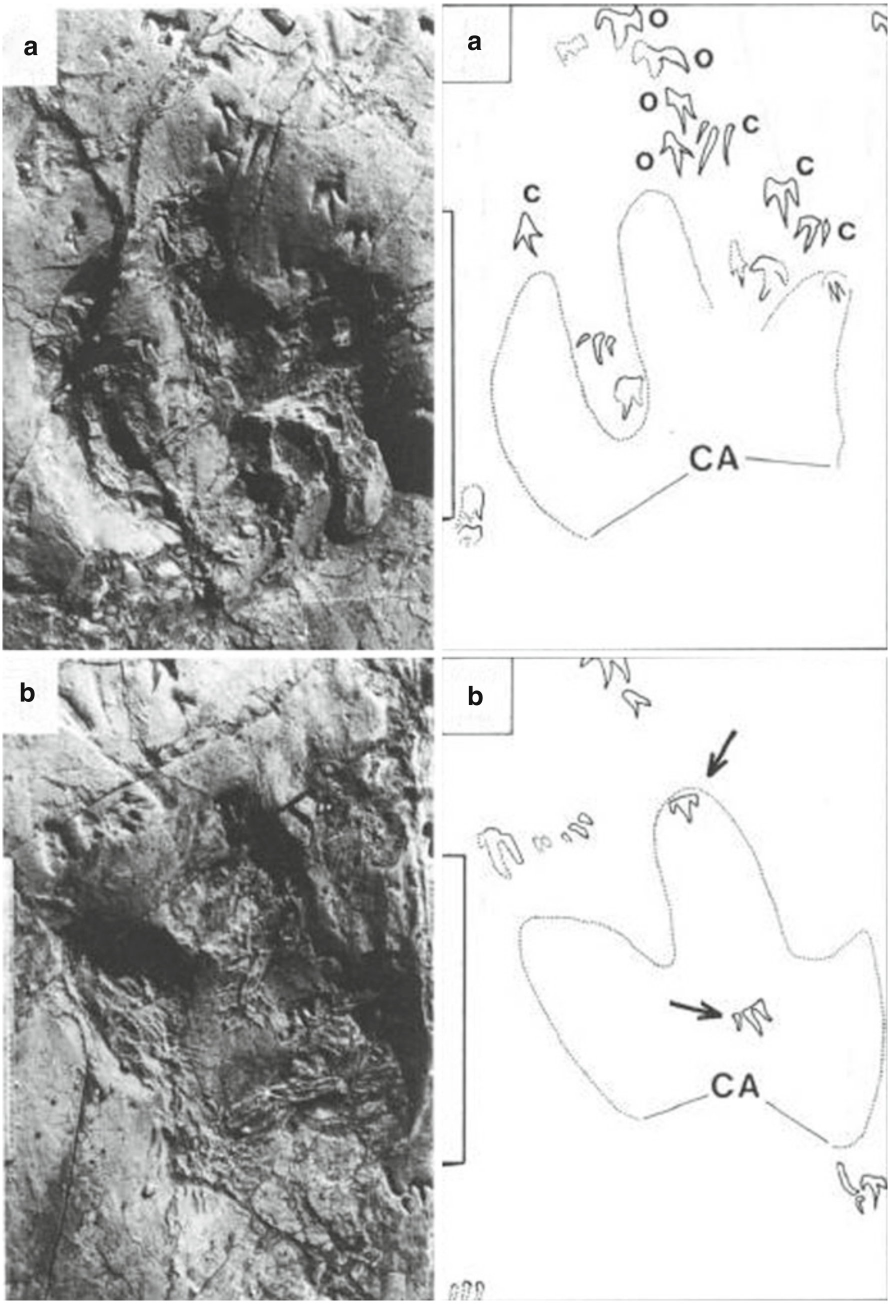

Fig. 10.1 The right (**a**) and left (**b**) footprints of a larger dinosaur, part of a track of 11 such prints, interpreted by some researchers as a predatory carnosaur (CA) and the footprints of many smaller ornithopods (*o*) and coelurosaurs (*c*). The smaller dinosaurs have been suggested to be members of a herd, fleeing from the larger predator (From Thulborn and Wade 1979)

behaviours onto the living members of clades and, by incorporating information about the evolutionary relationships between these extant species and their extinct ancestors, create statistical models which estimate the appearance (or disappearance) of this behaviour over evolutionary time.

The selection pressures which might favour grouping, including increased energy uptake through greater foraging efficiency, reduced risk of falling victim to a predator, more effective homeostatic regulation or collective travelling and greater offspring survival through communal or cooperative breeding, are discussed in some detail in Chaps. 4, 5 and 6. Clearly there are situations in which animals that are members of groups may be expected to do better than lone individuals, and depending upon the balance between the advantages and costs of grouping, there may likewise be circumstances where living alone is more beneficial. These advantages help make the case for group living being an adaptive strategy. However, if we wish to determine with any confidence that group living can arise through natural selection, we must demonstrate that a number of conditions have been met. Specifically, variation in tendency to form groups between individuals must exist, this variation must be heritable, and these individuals must live under conditions in which more sociable, group-forming individuals are more likely to produce more surviving offspring than those that are less gregarious or which do not group at all.

Accordingly, in this chapter, we consider evidence for consistently expressed variation in sociability within and between populations and evidence for heritability of this trait. We also look at variation in grouping behaviours at the species level, asking whether species respond to similar environmental challenges in similar ways. The comparative approach is valuable because it allows us to infer cases of convergence in grouping behaviour or, conversely, to determine the extent to which selection for grouping is phylogenetically constrained. Simulation models have also proven valuable in advancing our understanding of the evolution of grouping behaviour, particularly coordinated behaviour and the coevolution of prey and their predators. Finally we consider the role of the group itself as a selective environment and touch on some of the significant evolutionary consequences that may have arisen from group living, including disease resistance, social cognition and animal cultures.

10.2 Variation and Heritability

10.2.1 Intrapopulation Variability in Sociability

Individual variation is the raw material upon which natural selection acts. For researchers interested in the evolution of group living, a useful starting point might be one that considers the degree to which individuals differ in their tendency to associate with others and the extent to which such behaviour is transmitted genetically to their offspring. Animals of course vary in different aspects of their behaviour over their lifetimes and across seasonal cycles, as well as in the shorter term, as they react to predators, prey and other factors. Even when state-dependent and external factors are accounted for, there may still be differences between individuals in their behaviour. While such variation has long been realised, it is only in the last two decades that some behavioural ecologists have begun to focus heavily upon individual differences in behaviours, as well as the consistency with which these behaviours are expressed and the degree to which they are correlated with one another. The study of individual variation in the expression of behaviours, including aggression, neophobia, activity and, of relevance here, sociability, has given rise to a field of research termed animal personality or animal temperament (Sih et al. 2004a, b; Réale et al. 2007; Bell et al. 2009).

Focussing upon sociability, within-individual consistency and between-individual variation have been measured a number of different ways. One approach makes use of choice tests, in which subjects are given the opportunity to spend time associating with a group of conspecifics or with the larger of two or more such groups. Measures such as the proportion of time spent close to the stimulus group or some measure of the average distance maintained from it are used to provide a metric of sociability. By testing the same individuals on multiple occasions, researchers can look for positive correlations between successive association metrics in order to identify consistently more or less social individuals. Such an approach has been used to quantify consistency in shoaling behaviour in fishes, for example, in western mosquito fish (*Gambusia affinis*) (Cote et al. 2012), zebrafish (*Danio rerio*) (Way et al. 2015), three-spined stickleback (*Gasterosteus aculeatus*) (Dzieweczynski and Crovo 2011) and ninespine sticklebacks (*Pungitius pungitius*) (Webster and Laland 2015).

While choice tests represent a useful means of quantifying sociality, they suffer from a number of drawbacks. One is that they present the test subject with an idealised stimulus in the absence of potentially biologically relevant confounding variables. The other is that they negate the possibility of two-way choice, overlooking the fact that the process of group formation depends not only upon the focal joiner but upon the motivation or tendency of the other individuals to group as well. From an evolutionary perspective, the fitness returns from being highly sociable can only be realised if there are others with whom to group; in other words, the fitness potential of 'sociability phenotypes' might be frequency dependent. Social network analysis and associated statistical tools represent a means of overcoming these problems (Croft et al. 2008; Whitehead 2008). Free-ranging groups of captive or wild animals can be monitored, and the grouping behaviour of some or all individuals can be recorded and accounted for within the context of the distribution of grouping behaviours expressed by the rest of the group.

As with choice test approaches, research that has employed social network analyses can be used to explore within-individual consistency in sociability, the relationship between this trait and other behaviours. In a laboratory study using three-spined sticklebacks, social behaviour varied with boldness; bolder fishes were seen to spend less time associating with group mates than shyer fish, but tended to interact with a greater number of individuals overall (Pike et al. 2008). In contrast, in shoals of guppies (*Poecilia reticulata*) sampled in the wild, it was shyer fish that associated more widely (Croft et al. 2009b). The difference between these studies may arise for a variety of reasons, including differences in the assays used to determine boldness between the two studies. Nonetheless, it is clear that personality can have profound influence on individual patterns of association.

In great tits (*Parus major*), a model organism in the ecological study of animal personality, recent work has begun to explore the role of individual behavioural variation in shaping social interactions in wild flocks. Earlier research has identified that there are fast and slow explorer phenotypes within this species. Fast exploring birds, in addition to showing a greater tendency to investigate novel spaces and objects, are also more aggressive and risk-prone than are slow explorers (Dingemanse et al. 2004; van Oers et al. 2004; Carere et al. 2005). This variation, which has some genetic basis, is maintained in the wild by fluctuating selection pressures linked to yearly variation in environmental conditions favouring different behavioural phenotypes (Dingemanse et al. 2004). Based on selection experiments in which lines of great tits were bred for two generations for high and low risk-taking behaviour, which has been shown to be positively correlated with exploratory behaviour, van Oers et al. (2004) estimated a realised heritability of around 20 % for this behaviour. Work with a PIT-tagged wild population of great tits has also revealed that fast and slow explorers differed markedly in their sociality. Fast explorers tend to interact with many other individuals, albeit for shorter time periods, to move frequently between flocks and to be more likely to be found at the periphery of the flock. In contrast, slow explorers interact more frequently, but with fewer individuals, and exhibit greater flock fidelity (Aplin et al. 2013, 2014). Taken together, these studies demonstrate that behavioural syndromes, which have a significant heritable component, can have a considerable influence upon aspects of grouping behaviour.

10.2.2 Interpopulation Variation in Sociability

Animals whose ranges span different regions with varying environmental conditions might be expected to exhibit associated variation in their grouping behaviour. This idea has been borne out by studies in which researchers have examined the grouping responses of individuals from different populations under uniform conditions. Guppies (also discussed in more detail below) show population-level differences in shoaling behaviour that reflect the level of predation pressure under which they have evolved. Botham et al. (2008) compared the shoaling and other behavioural responses of guppies from seven different populations to each of four different predators that differed in the threat that they posed. They reported an interaction effect between predator type and the predation pressure that the population was exposed to; guppies from higher-predation populations spent more time shoaling when in the presence of the most dangerous of the four predators.

Studies such as this type are informative because they demonstrate the potential for populations to exhibit variation in the grouping behaviour even when exposed to a common environment. In testing animals taken directly from the wild however, it is difficult to infer the relative contribution of inherited versus developmental effects or experience. Behavioural responses can be plastic, and whether it be through learning or through environmentally induced developmental responses, animals that have been exposed to high- or low-predation risk previously might tend to react differently when encountering predators subsequently than would predator-naïve individuals from the same populations. Different approaches can be used to estimate the contribution of genetic inheritance relative to these other factors. One is to take animals from different populations and breed them, rearing their descendants under common conditions. If behavioural differences persist in their offspring, and maternal effects can be accounted for or ruled out (for example by focussing upon second-generation descendants, whose parents were also reared under controlled conditions), then it can be inferred that the behaviour has a heritable component. Crosses can be performed between populations in order to identify the genetic basis of the traits of interest.

Another approach that has been adopted by researchers is the translocation experiment. Animals can be taken from one location and introduced into another, where different selection pressures prevail. Here, it is predicted that different characteristics should be selected for and that there will be gradual divergence between the ancestral and translocated populations with respect to these traits. Researchers can test this prediction by measuring changes over time both in the traits themselves and in the relative frequency of the genes with which they are associated. Translocation experiments are useful in that they expose the translocated animals to a full suite of natural (as oppose to artificial) selection pressures. Downsides include the fact that such experiments cannot usually be replicated to anything like the same degree as can be achieved with laboratory rearing designs. There may also be significant environmental and ethical considerations; once introduced, the animals and their descendants may be difficult or impossible to remove again, they may interbreed with resident populations and they may have other detrimental impacts upon local ecology. Mesocosm studies, in which animals are reared under seminatural conditions in artificial or enclosed areas of habitat, represent a compromise, allowing for both ecological realism and replicability while avoiding some of the costs associated with translocations.

Experimental investigations of shoaling in guppies and sticklebacks provide useful case studies of the role of selection in shaping grouping behaviour. In the case of guppies, both translocation experiments and comparison of captive-bred decedents have been used. In sticklebacks, crosses have been performed between divergent populations in order to uncover the role of selection on behaviour and the neurosensory system in determining aspects of shoaling. In another fish species, zebrafish, heritability estimates for shoaling behaviours have been estimated. Work in birds has focussed upon heritability of group size preferences within the context of breeding colony size selection by swallows and falcons. These case studies are discussed in more detail in the sections that follow.

10.2.3 Shoaling in Fishes

Exactly the kind of translocation experiment described above has been carried out, using guppies. The streams of the Northern Range of mountains in Trinidad are divided into high- and low-predation sites by the presence of waterfalls. In some of these streams, guppies occur both up- and downstream of the falls, while their fish

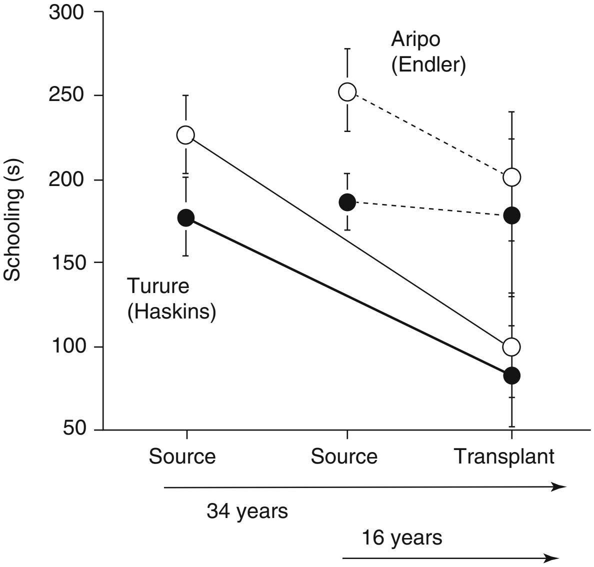

Fig. 10.2 Guppies from two high-predation rivers were transplanted into low-predation rivers. After 34 and 16 years, respectively, the offspring of fish from the source population and from the transplanted populations were tested for schooling behaviour. Both males (*black circles*) and females (*white circles*) from the transplanted populations spent less time shoaling compared to fish from the source populations. This effect was only significant for the Turure population (From Magurran 1998)

predators are by and large restricted to channels downstream of these natural barriers. Guppies below the falls are subjected to greater predation risk and accordingly differ from those found upstream in a range of life history traits and morphological and behavioural adaptations. In 1957, guppies were transplanted from a high-predation stream in the Caroni drainage to a low-predation and previously guppy-free channel in the Orapuche drainage. Later, in 1976, guppies were moved from the high-predation Aripo River to one of its tributaries, where fewer predators occurred (Reznick et al. 1990; Magurran 1998, 2005). Reznick et al. (1990) periodically measured various life history traits in the fish that were translocated in 1976, reporting that over an 11-year period the descendants of the translocated fish came to mature later and at a larger size and produced larger offspring. Magurran and co-workers focussed upon antipredator behaviours, including shoaling (Magurran et al. 1992, 1995; Carvalho et al. 1996). Studying fish from both of the two translocations, they showed that guppies of both sexes in the 1957 translocation showed a marked reduction in the time that they spent shoaling with others compared to fish from the river from which they originated. In the case of the more recent 1976 introduction, a non-significant trend towards reduced shoaling was recorded. At the time that these experiments were performed, 34 and 16 years had passed since the translocations occurred, corresponding to approximately 60 and 30 guppy generations, respectively. The shoaling tests were performed on the laboratory-bred offspring of guppies that were collected from the sites of the introduced populations and from the original source populations, allowing developmental effects to be controlled for. These studies provide a neat demonstration of the impact of natural selection, in this case release from predation, upon grouping behaviour (Magurran 1998, Fig. 10.2).

Researchers have also taken the approach of breeding from guppy populations living under different predation regimes and rearing lines of descendants under common conditions in order to infer selection for traits including tendency to shoal.

For instance, Magurran et al. (1992) demonstrated significant variation in the time spent shoaling by laboratory-bred offspring of guppies from seven populations. In another study, Huizinga et al. (2009) investigated the interaction between plastic response environmental cues and the genetic predisposition of shoaling behaviour in guppies. They compared the shoaling responses of second-generation, laboratory-bred fish from high- and low-predation sites for each of two naturally occurring populations. They found that for both populations the high-predation-site fish shoaled more cohesively than the low-predation-site fish. High- and low-predation-site fish responded to cues associated with predation risk by forming denser groups, with the high-predation-site fish shoaling more tightly. This demonstrates that while shoaling responses are affected by cues in the external environment, response plasticity is mediated through interactions with inherited variation in behaviour.

Like guppies, three-spined sticklebacks have proven to be a valuable model organism in evolutionary ecology. They have a broad distribution within the temperate northern hemisphere and inhabit a range of habitats, from marine coasts and salt marshes to rivers and streams and the margins and pelagic regions of lakes. There has been substantial adaptive radiation as populations have colonised new habitat types, producing striking variation in morphology, life history and behaviour (Ostlund-Nilsson et al. 2006; Hendry et al. 2013). This variation includes shoaling, which can vary markedly between populations. Wark et al. (2011) compared the shoaling behaviour of sticklebacks from marine and lake benthic habitats. These authors used a novel apparatus in which a shoal of model sticklebacks was suspended from a turning wheel placed above a circular tank. Each model stickleback in the shoal was made from a cast of a benthic x marine hybrid. The whole shoal could be made to swim circuits of the tank, presenting a consistent and precisely controllable stimulus to the test subjects. It was revealed both that the marine fish spent more time shoaling with the model stickleback shoal and that they remained oriented more closely with it than did the benthic fish. By rearing captive benthic and marine fish in mixed groups in the lab and then quantifying their social behaviour, these researchers were able to show that the observed differences in shoaling behaviour persisted, demonstrating that it was inherited and was not solely based upon learning or experience. In the following work, the same team performed quantitative trait locus analysis on shoaling behaviour of F2 hybrids of marine and benthic sticklebacks. They found that the tendency to shoal was under the influence of one genomic region, while the tendency to orientate with a moving group was controlled by another region, affecting the development and structure of the lateral line system (Greenwood et al. 2013). Shoaling behaviour in sticklebacks then has evolved through selection both upon the behaviour itself and upon the neurosensory system, through which it is mediated (Wark et al. 2012; Greenwood et al. 2013).

Wright et al. (2003, 2006) investigated the genetic basis of shoaling behaviour in zebrafish. In an initial study (Wright et al. 2003) compared shoaling in the laboratory-reared offspring of four natural populations. No differences were seen between these. In focussing upon one of these populations in more detail, however, they were able to estimate the heritability of shoaling tendency in these fishes at 0.40, a reasonably high level for heritability in a behavioural trait, although it should be noted that the error estimate in this case was high. A second study (Wright et al. 2006) demonstrated substantial differences in time spent shoaling and willingness to approach novel objects, a measure of boldness, by zebrafish descended from a wild population and a laboratory strain. They were able to identify quantitative trait loci, stretches of DNA containing the genes that affect these behaviours, in several genomic regions.

10.2.4 Colonial Breeding in Birds

The above examples focus upon the formation of mobile groups. There is also evidence that propensity to breed in colonies has a heritable component in some bird species. Cliff swallows (*Petrochelidon pyrrhonota*) form breeding colonies ranging in size from tens to thousands of nests. Brown and Brown (2000) showed that birds preferred to breed in colonies similar in size to the ones that their parents bred in, with cross-fostered birds, translocated as eggs from parental nests in large colonies to foster nests in small ones, or vice-versa, still preferring to breed in colonies that were similar in size to the one of their birth. This work was extended by Roche et al. (2011). They confirmed that cross-fostered swallows showed a preference for colonies similar in size the ones their parents selected, early on in their own lives. However, in subsequent years, birds that were born in smaller colonies but translocated to larger ones became more likely to select larger colonies themselves. The authors suggest that there may be a strong genetic effect upon colony size preference early in life, favoured by selection because it enables individuals to better match their phenotype to the social environment. Over time however conditions may change and the birds gain experience and have access to information about the quality of different colony sites. A degree of flexibility in colony size selection may therefore be favoured by selection.

Lesser kestrels (*Falco naumanni*) also breed colonially, and there is heritable variation in colony size preference, estimated to be as high as 0.53 by Serrano and Telle (2007). Colony size preferences are typically not apparent until birds are older than 3 years old. This is both because older birds arrive at the breeding sites sooner than younger ones and also because, being larger and heavier, they are able to outcompete and physically exclude them from colonies. As a consequence, the colony sites used by younger birds may not reflect their preferences. By the age of three however, they have reached their maximum body size and mass and are better able to compete for breeding sites.

10.3 Phylogenetic Perspectives on the Evolution of Group Living

For researchers interested in the evolution of group living, simply comparing populations or species and attempting to relate the extent to which they form groups to currently prevailing selection pressures may not be sufficient to gain insight into the distribution of these behaviours. This is because behaviour may not be free to rapidly adapt to local conditions; instead, it may be constrained by previous selection that has occurred earlier on in the lineages that today's species are descended from. Here, statistical approaches that account for phylogeny, the patterns of relationships between species (and within species, between populations), can be useful. By quantifying the extent to which living species form groups, and mapping this information onto phylogenetic trees based upon molecular, morphological or other data, researchers can estimate for a given clade the likelihood that grouping has evolved recently or whether it is an ancestral trait inherited from an earlier common ancestor. In fact just such issues have dogged comparative approaches to studying the evolution of group living in primates and antelopes. In both cases, early work placed heavy emphasis upon adaptation to the social and physical environments experienced by contemporary species within these groups, while failing to account for phylogeny. When later researchers applied phylogenetic approaches, phylogeny was found to explain a significant amount of the variation in grouping behaviour exhibited by contemporary species within these groups. In primates and antelopes, as well as in flock-forming birds, both phylogeny and adaptation to selective pressures have been inferred in influencing the evolution and the loss of grouping behaviour. Phylogenetic approaches have also been used to investigate the role of kin selection in the evolution of cooperative breeding, both in eusocial insect and in vertebrates. These cases are discussed in more detail below.

10.3.1 Eusocial Insects

Eusociality is an extreme social system in which the majority of the members of a colony forgo reproduction in order to raise the offspring of a minority of individuals. Recent years have seen debate between researchers over the role of kin selection in the evolution of eusociality. Proponents have argued that eusociality arose because multiple helpers greatly increases the number of offspring that could be reared and, crucially, because those helpers were very closely related to the breeding individuals and therefore to the offspring. By helping to raise these offspring, they gained inclusive fitness payoffs that exceeded the combined direct fitness that the helpers might have achieved through attempting to breed alone (Queller and Strassmann 1998). Other researchers have downplayed the role of kin selection. Wilson and Holldobler (2005), for example, have noted that the average degree of relatedness among colony members of some species of eusocial insects can be quite low. They have argued that the high average relatedness seen among members of colonies of other species is a consequence of low rates of dispersal of young and that kin selection and inclusive fitness have not played a role in driving the evolution eusociality. This position was pursued in a controversial paper by Nowak et al. (2010), in which the authors modelled the evolution of eusociality. They concluded that the concept of kin selection has proven to be of limited use. Instead, these authors argue that the evolution of eusociality can be better understood within a population genetical framework. This paper has been criticised by a number of researchers, leading to one of the biggest kerfuffles of recent times in evolutionary biology. Abbot et al. (2011), Boomsma et al. (2011) and Strassmann et al. (2011) argue that Nowak and colleagues' work overlooks several decades of empirical evidence. Boomsma et al. (2011) in particular note a failure to address evidence from empirical studies using phylogenetic analyses that demonstrates that eusociality has only evolved in clades where the conditions for kin selection were likely present and where low average relatedness among colony members among some extant species is likely a derived and not an ancestral condition (Hughes et al. 2008). As of the time of writing, the debate continues apace (Liao et al. 2015; Nowak and Allen 2015).

Hughes et al. (2008) specifically investigated the role of ancestral monogamy in the evolution of eusociality in hymenopteran insects using data on female mating frequencies. Ancestral monogamy, in which a female mates with only one male, is thought to be a key factor in facilitating the evolution of cooperation over rearing young between a breeding female and her nonbreeding adult offspring. This is because helpers are as closely related to their younger siblings as they would be to their own potential offspring. Cooperative breeding may then evolve if it leads to more offspring surviving than does independent reproduction by each helper. Hughes and co-workers compared the number of males that females typically mated with for 267 species of eusocial wasps, bees and ants. Performing phylogenetic analyses, they found strong evidence that female monogamy was likely the ancestral condition in each of the eight eusocial lineages they looked at. In those species within the lineages where females do mate with multiple males, evidence suggests that this condition is derived and not ancestral. Hughes et al. (2008) argue that these findings are incompatible with the idea that high relatedness between colony members represents a consequence of limited dispersal in species that evolved eusociality through mechanisms dependent upon direct fitness alone. Instead, eusociality appears to have evolved through kin selection, made viable by ancestral monogamy.

10.3.2 Cooperative Breeding in Birds

Cooperative breeding occurs in a range of species, when breeding territory holders are assisted in the raising of their young by other individuals that forgo some or all of their own reproductive potential. Helpers may or may not be related to the breeders, and the roles assumed by the helpers vary between species, but may include feeding the young, looking out for predators or defending the territory from rivals. Female monogamy has been shown to be of importance in the evolution of cooperative breeding in birds, in cases where the helpers are the adult offspring of the breeding female. If the female is monogamous, mating with only the father of the would-be helper, then the helper will be equally related to its younger siblings as to any young that it itself may produce. If females are highly promiscuous on the other hand, then the average relatedness of a helper to its mother's offspring will be lower than its relatedness to its own offspring (Boomsma 2007). Whether cooperative breeding evolves or not then will depend upon a combination of the helper's relatedness to the young it is assisting in raising, the likelihood of these young surviving with the helper's assistance, and the likelihood of the helper's own young surviving were it to attempt to breed independently. In marginal environments and in the face of severe pressure from predators or brood parasites (Feeney et al. 2013), one pair of parents may not by themselves be able to successfully rear young. Under such conditions, the inclusive fitness returns of helping raise siblings might exceed the direct fitness of breeding oneself, and selection may be expected to favour cooperative breeding.

Cornwallis et al. (2010) investigated the role of monogamy in the evolution of cooperative breeding in birds. The importance of monogamy in facilitating cooperative breeding has been uncertain in vertebrates. This is because lifetime monogamy is rare, and extra-pair copulation is common even within pair-breeding species (Westneat and Stewart 2003). Also fitness benefits gained from cooperative breeding interactions do not necessarily require high levels of relatedness between interacting parties (Clutton-Brock 2002), while cooperation may actually facilitate promiscuity, by freeing females from reliance upon their mates who might abandon them if they are cuckolded (Mulder et al 1994). Through phylogenetic analysis of 267 bird species, Cornwallis et al. (2010) revealed that cooperative breeding arose more often in lineages where promiscuity was low. Cooperative breeding was also seen among some lineages containing moderately promiscuous species. Earlier work has revealed evidence that helpers can discriminate between young on the basis of their relatedness, directing help towards young that are more closely related to them (Griffin and West 2003). Cornwallis and co-workers were able to explore the relationship between kin discrimination, promiscuity and cooperative breeding in their data set. They found that the strength of kin discrimination was greatest in species where promiscuity was intermediate. Very high and very low promiscuity will result in little variance in relatedness between a helper and its siblings; they will all tend on average to be closely or more distantly related to the helper, respectively. Where promiscuity is intermediate however, the helper may encounter, for example, both full and half siblings. Faced with such variation, selection may favour kin discrimination and facilitating selective provisioning of more closely related chicks. Data for birds then upholds the monogamy hypothesis for the evolution of cooperative breeding; this behaviour has evolved because it confers inclusive fitness benefits to helpers.

10.3.3 Herd Sizes of African Antelopes

The previous two examples have dealt with cooperative breeding. Phylogenetic approaches have also been employed to study the evolution of grouping more generally. Often, these have been applied to data that has already been explored from a socioecological perspective and serve to demonstrate the importance of considering phylogeny when investigating the distribution of behaviours across species.

In 1974, Peter Jarman published what was to become an influential paper in which he presented data on the relationships between body size, diet selectivity, use of open habitat, response to predators and group size for 75 species of African antelopes. These were classified by feeding type. The first category contained the most selective of browsers that feed upon more protein-rich parts of plants. The second category contained browsers that feed on new growth of grasses and newly produced shrub leaves. The third and fourth categories contained those that feed selectively but widely on grasses and browse and generalists that feed on a wide variety of grasses. The final category contained the most general of feeders that unselectively consume both grasses and browse. In general, the most selective foragers tended to be smaller in size. Linking this to group size, he presented data showing that smaller-bodied selective browsers tend to form the smallest groups, while larger, less-selective and generalist browsers and grazers occurred in larger herds. Jarman suggested ecological explanations for these observations. The protein-rich seeds and fruits favoured by the smaller-bodied antelopes are often patchily distributed within the stands of shrub or woodland upon which they grow. This means that competition is likely to be greater for them, favouring single individuals, pairs or very small groups occupying feeding territories. The grasses fed upon by less-selective grazers are more widely distributed and, at certain times of year at least, are effectively inexhaustible. Here, competition for food is less likely to be a limiting factor upon group size, and larger herds ranging over wider areas should therefore be expected. Predation risk too should bear upon group size. Larger-bodied antelopes living in open country may be more readily detectable to predators, again selecting for larger group sizes. The herds' main defences against predator attacks include running away or, if they are numerous enough or if the threat posed by the predator is not too severe, defensive behaviour to drive the predator off. In contrast, smaller antelopes living among the cover of light woodland might rely more upon camouflage or the opportunity to hide in order to avoid their predators. This may be enough to offset the benefits of grouping, and smaller groups or lone animals might actually do better than larger herds, by being less conspicuous. Jarman concluded then that the most important factor determining group size in antelopes is their feeding type and, indirectly, by driving habitat use, exposure to different levels of predation pressure.

Jarman's (1974) work was revisited and extended by Brashares et al. (2000). These authors noted that one of the limitations of Jarman's (1974) original study was that it failed to account for phylogeny. They reanalysed the data set, using statistical approaches that were not available to Jarman in 1974. In accounting for phylogeny, Brashares et al. were able to investigate whether behavioural traits such as species' average group size represent convergence via adaptation to similar selective environments or whether they are an artefact of shared evolutionary history. In the latter case, two species may express similar traits such as tendency to form large groups not because they have evolved such behaviour independently in response to similar selective pressures but because they have inherited it from a common ancestor that also tended to form large groups.

Brashares et al. (2000) first performed conventional (i.e. non-phylogenetic) analyses of the antelope data. Their findings echoed Jarman's (1974), in that they found that more selective feeders tended to be smaller in body size than more generalist

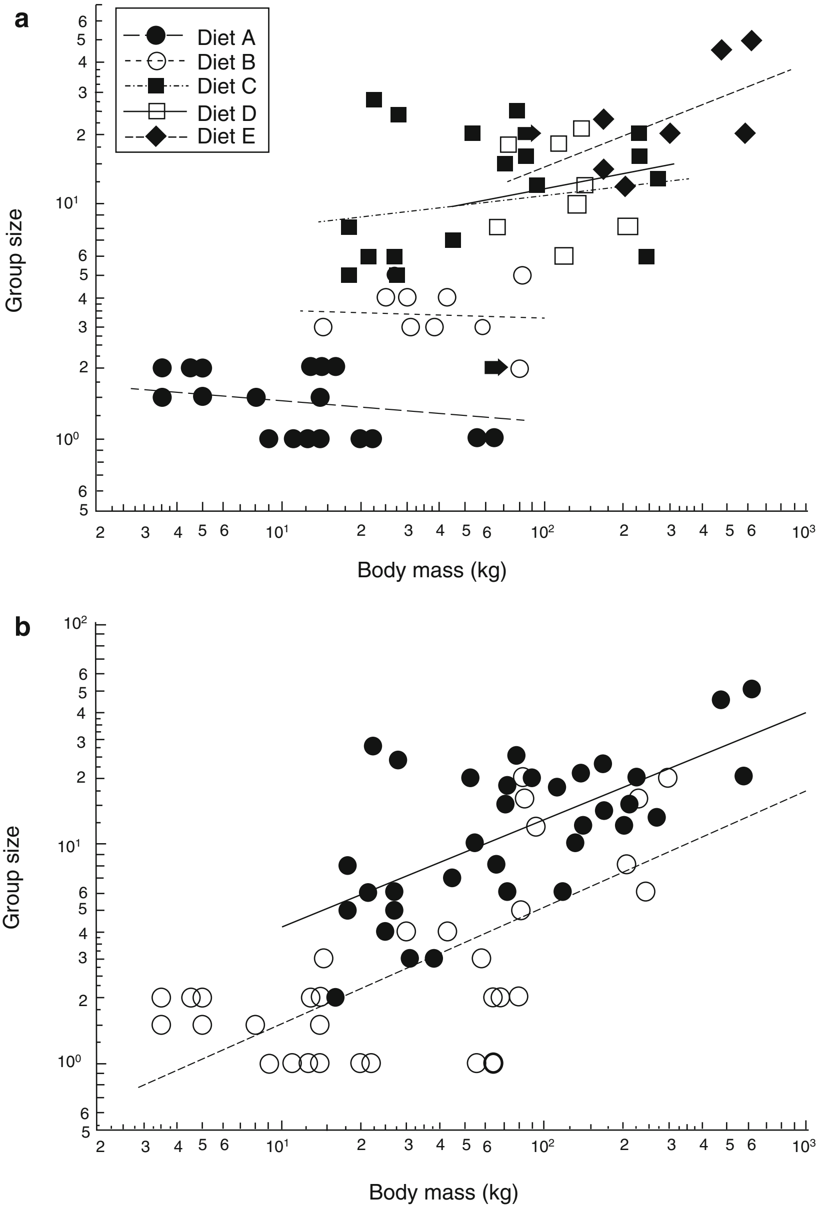

Fig. 10.3 (**a**) Among antelopes, more selective feeding species tend to be smaller in size and tend to live in smaller groups than generalists (see main text for description of dietary classifications). (**b**) Species that flee from predators (*black circles*) tend to live in larger groups than do species whose main defence is to hide in cover (*white circles*) (From Brashares et al. 2000)

grazers and browsers, that the generalists tended to form smaller groups and that the smaller selective feeders were more likely to rely upon hiding to evade predators, while the larger generalists predominantly either fled approaching predators or actively defended themselves against them (Fig. 10.3). In subjecting these data to phylogenetic analyses, it was seen that the relationships between body size and feeding selectivity and group size and feeding selectivity persisted, as did the relationship between group size and fleeing versus hiding from predators. However the relationship between body size and group size was substantially weakened when phylogeny was taken into account, remaining only marginally positively correlated in analyses that considered all 75 species together, while no relationship was present when the seven antelope tribes represented in the sample were considered separately (Fig. 10.4). Brashares et al. (2000) acknowledge that for some of these tribes the sample sizes were low, resulting in low to moderate statistical power, meaning that it cannot be ruled out that such a relationship between body size and group size may have been overlooked for some tribes.

Some researchers have been critical of other aspects of Jarman's (1974) study. Kingdon (1982) suggested that the categories of feeding selectivity to which the antelope species were assigned were not realistic and that some behaviours assumed to be fixed at the species level actually vary between populations. Estes (1991) points out that group size for a given species can vary greatly between locations and across seasons. Assigning mean values for group size and other behaviours for each species can lead to within-species variation, for example, between divergent populations, to be overlooked. Finally, Brashares et al. (2000) argue that even if this variation was to be incorporated into finer-grained analyses, it could be challenging to parse out the effects of plastic responses to local environmental conditions and genetic adaptations. These concerns highlight limitations that can sometimes apply when conducting phylogenetic analyses: data is often drawn from other studies by meta-analysis, and the authors of these primary studies may not have collected data using the same approaches and may have collected data on varying numbers of individuals. While these effects can be accounted for statistically, it may also mean that data sometimes must be compiled into loose categorical variables (as in Jarman's (1974) feeding classifications). It may also mean that where entire species are represented by data from only one or a few populations, important within-species variation is lost, and the resulting analyses are of a lower resolution than they otherwise might be.

10.3.4 Primate Group Size and Structure

The evolution of primate group social structure has long interested researchers because of the unusual afflictive bonds and patterns of group stability shown by some species and because of what it can potentially tell us about the social evolution of our own species (Di Fiore and Rendall 1994; Shultz et al. 2011). Paralleling the approach taken by Jarman (1974) in his investigation of African antelope group size evolution, early investigations of primate group size and structure focussed upon relationships with habitat use, noting that nocturnal and arboreal species tend to live alone or in smaller groups, while the largest groups are often found among diurnal, predominantly ground-dwelling species (Crook and Gartlan 1966). Predation may be expected to be higher in open habitats, suggesting that this may be a driver of large group sizes in species found in the open. Wrangham (1980) placed emphasis upon the role of competition and the ability of larger groups to supplant smaller

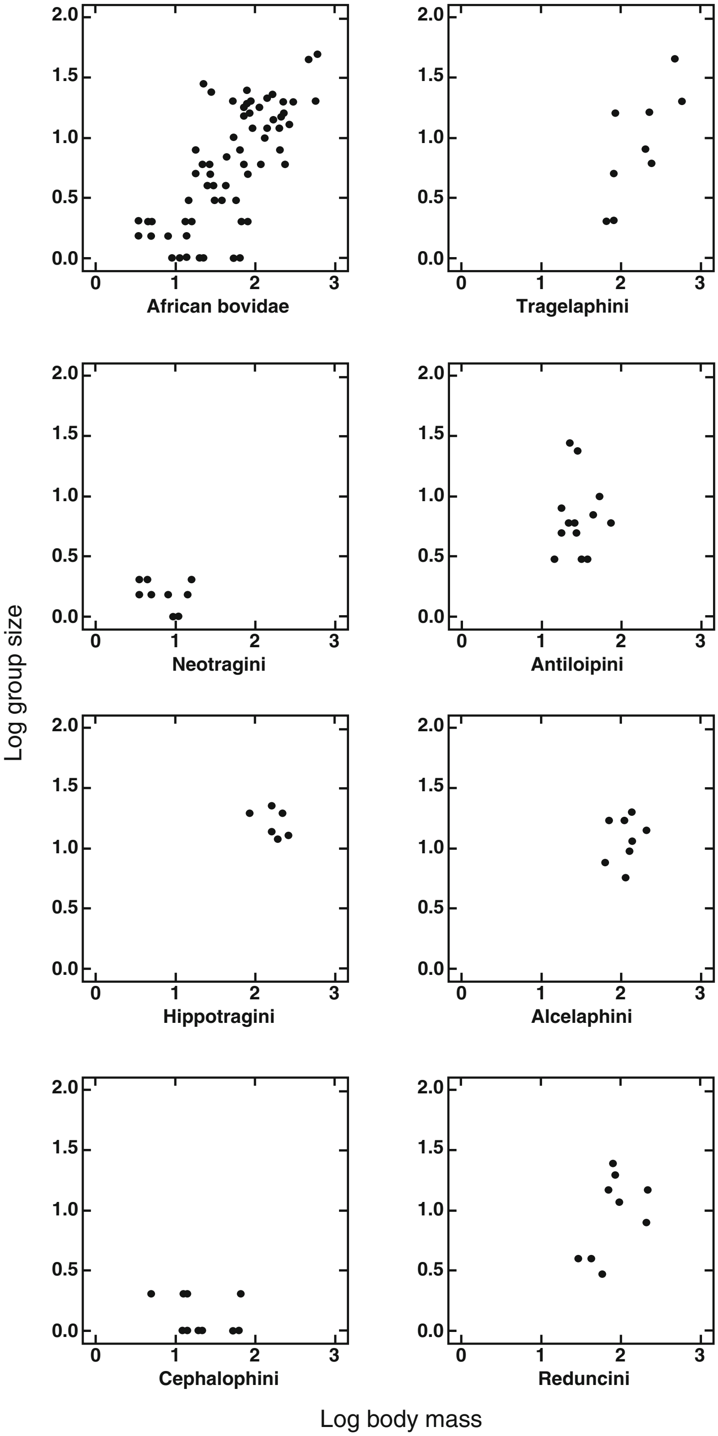

Fig. 10.4 Body mass and group size are correlated for species within Bovinae subfamily, but not for species within seven tribes of the Antilopinae subfamily (From Brashares et al. 2000)

ones from resource patches as driving group size in some species. Noting that competition alone may be insufficient to explain group living, since groups are found even in habitats where competition for resources is not thought to be intense, other researchers advocated the combined effects of competition and response to predation pressure in determining group living (van Schaik 1983, reviewed by Clutton-Brock and Janson 2012; Beauchamp 2013).

More recently, researchers have approached the question of primate grouping behaviour using methods that examine both ecology and phylogeny (Di Fiore and Rendall 1994; Shultz et al. 2011; Clutton-Brock and Janson 2012). Phylogenetic analyses have revealed that many Old World primates have very inflexible social structures and that much of the variation in social behaviour seen between species can be accounted for by shared ancestry. In fact, social structure is strongly conserved among closely related species, even where they occupy ecologically dissimilar environments (Di Fiore and Rendall 1994). An analysis by Shultz et al. (2011) considered 217 Old and New World primate species using a phylogenetic tree assembled from genetic data. These authors too found that grouping behaviour exhibited a strong phylogenetic signal in most lineages, suggesting that it has been inherited from earlier common ancestors rather than arising as an adaptive response to the local environment. Flexibility in social structure was only seen in two groups, the Lemuridae, the lemur family, and the Callitrichidae, a New World family that includes the marmosets and tamarins.

Building on this, Schultz et al. (2011) then fitted evolutionary models to their data in order to determine which evolutionary scenarios best described the variation in social organisation observed today. Using this approach, they were able to discount the socioecological account of primate group structure evolution, in which group structure is facultative and responsive to environmental conditions. They also found that a stepwise model in which group structure progressed from solitary living to pair formation to larger more complex groups was not well supported. In fact, the best supported model was one in which solitary living was followed by the appearance of larger single-sex groups. From these, male-female pairs and harems consisting of one male and multiple females evolved. Single-sex groups are estimated to have appeared around 52 mya in the simian lineage and 32 mya in the prosimians. Harems appeared in the Colobinae and Cercopithecini 16 and 14 mya, respectively, while pair living arose in a number of different lineages multiple times between 8.6 and 4.5 mya. Their analysis also provides strong support for models positing a shift from nocturnal to diurnal activity (and possibly resulting in exposure to greater predation pressure, or exposure to different types of predator) as being associated with the transition to group living. The role of sex-biased dispersal was also considered. Models incorporating an association between the onset of sociality and sex-biased dispersal were more poorly supported than those linking sociality to diurnal activity. The best supported models predicted that ancestral dispersal patterns were bisexual (i.e. both sexes dispersed from the natal range) and that sex-biased dispersal only appeared after the onset of group living in primates.

In primates then, grouping behaviours are strongly influenced by evolutionary history and are highly conserved in many lineages. The transition to daytime activity and with its exposure to greater predation pressure may have first driven the evolution of group living. Subsequently, selection pressures arising from the social environment have led to the diversity in primate group social structure seen today, including convergent evolution of harems, pair living and sex-biased dispersal from natal groups.

10.3.5 Flocking in Birds

Beauchamp (2002) investigated the evolution of social foraging in birds. He focussed upon birds that specifically flock when foraging, as opposed to coming together to breed or migrate, classifying flocks as groups consisting of three or more individuals of the same species. Employing phylogenetic analyses, he revealed that flocking has independently evolved in 17 different clades. Moreover, reversion to solitary foraging has also evolved a number of times in clades where flocking had previously evolved. Flocking appears to have evolved more often among clades containing species that forage for patchily distributed resources such as fruits and seeds. The evolution of flocking was not associated with habitat openness, which may suggest that social foraging has played a stronger role than predation pressure in driving this behaviour. Finally, flocking also appears to have evolved more often in families with larger-sized species. Beauchamp (2013) acknowledges some limitations to this study. He points out that there are far more species represented within the clades considered in his study than there are in similar antelope and primate studies (discussed above) and that some phylogenetic relationships, even between some families, are also poorly resolved and may be subject to revision in light of future research.

10.4 Simulating the Evolution of Grouping and Coordinated Behaviour

Phylogenetic methods can allow researchers to reconstruct the appearance, disappearance and contemporary distribution of grouping behaviours, but using these approaches cannot always reveal why such behaviour evolves. Here, simulation models that take into account both predator sensory perception and ability to process information on prey distribution and movement and the survival of prey as a function of the grouping behaviours that they perform and co-evolutionary interactions between the two have provided useful insights.

Olson et al. (2013) created a series of simulation models to explore interactions between prey aggregation and predator hunting strategies, showing that predator confusion effects, limitations upon the ability to process information on the movement of large numbers of prey simultaneously, may be sufficient to select for swarming behaviour in prey. In their simulations, mobile predators and prey were able to perceive one another within a field defined by a finite angle and range. Predators moved through the environment, detecting prey that moved through their field of perception, and attacking those that passed with a fixed distance. Prey were able to discriminate between other prey and the predator and could switch between stopping and moving forward, left or right. Predators followed these movement rules too, but moved faster and turned more slowly than the prey. In some simulations, the predators were also subject to confusion effects. These were simulated by implementing a constraint on the predator's likelihood of capturing targeted prey individual. The confusion constraint was applied when other prey items were close to the targeted prey, so long as they were within the predator's perceptual range. The strength of the confusion effect suffered by the predator was dependent upon the number of prey that was close to the target. The predator had to wait a fixed period of time (the handling time) between launching attacks. Selection was accounted for within the simulations using a genetic algorithm. The movement of predators and prey was controlled through a Markov network which produced movement decisions by incorporating both information on the presence and location of other agents and memory. Markov networks that maximised prey intake were selected for in the predators, while in prey, behaviour that prolonged survival was favoured.

The inclusion of a confusion effect in conjunction with handling time created a selective environment which favoured swarming by prey. Accordingly, swarming behaviour was not seen in iterations of the simulation in which no confusion effect was included; instead, prey tended to disperse so as to avoid the predator. In contrast, in runs where confusion effects were present, prey evolved grouping behaviours in the majority of cases. These were diverse and included the formation of large, elongated swarms in which prey followed neighbours in front of them and smaller compact swarms in which the prey circled around their neighbours (Fig. 10.5). Prey density after 1200 cycles of selection was significantly higher in runs with predator confusion effects than in those without, where in fact prey dispersal was selected for, suggesting that predator confusion can drive swarming responses. Predator hunting strategies varied depending upon the presence or absence of confusion effects too. With no confusion effects, they simply pursued the nearest prey until it was captured. With confusion effects however, they tended to focus upon peripheral prey when attacking groups. This served to minimise the number of prey within the predators' perceptual field, reducing the confusion effect and increasing capture rates. In simulations where the predator's perceptual field was free to evolve, they found that forward-oriented field with narrow but high resolution systems was favoured. Olson et al. (2013) conclude that the existence of confusion effects is sufficient to generate selection for a range of swarming responses in prey and that these in turn generate selection upon predator perceptory systems, leading to coevolution between the two.

Adopting a novel, hybrid approach, Ioannou et al. (2012) presented simulated prey to real predators, in order to determine the extent to which coordinated behaviour affected likelihood of being attacked. The prey took the form of moving dots, projected onto the wall of a glass fish tank, which contained a predatory bluegill sunfish (*Lepomis macrochirus*). The prey dots varied in the extent to which they were attracted to and aligned with one another. Where prey was strongly attracted to each other and tended to align, they formed coordinated groups. In contrast, for prey where these parameters were weak, they tended not to aggregate and their

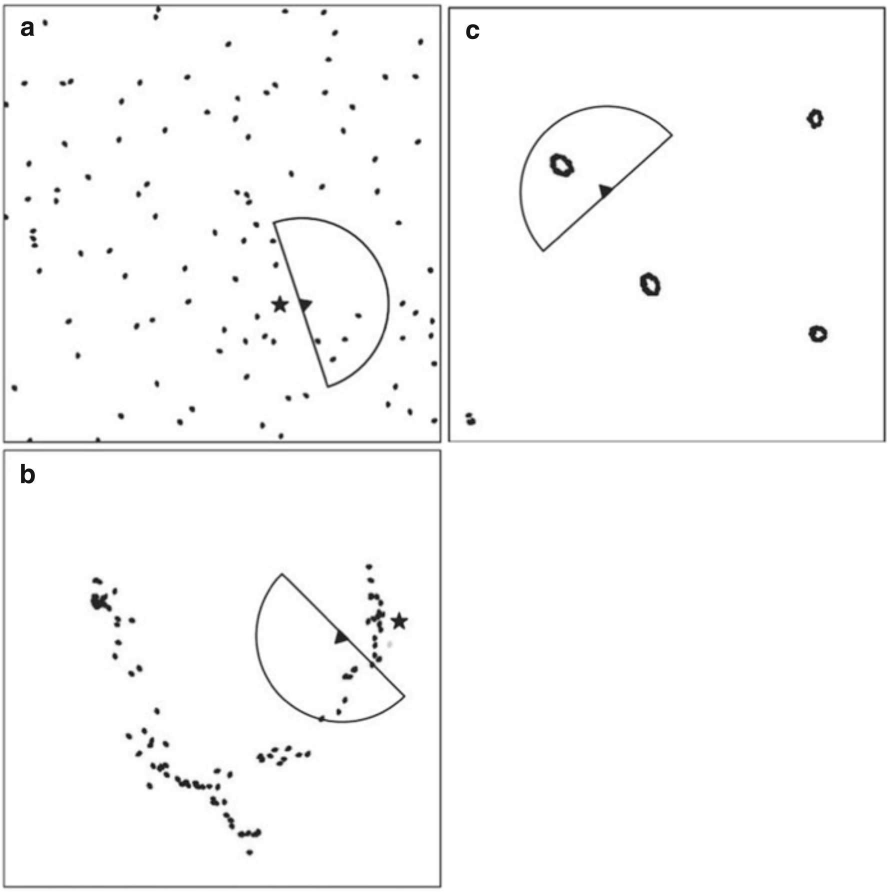

Fig. 10.5 Screen captures from simulation model runs investigating the role of predator confusion in the evolution of prey swarming behaviour. (**a**) With no predator confusion, prey tends to disperse. (**b**) In some runs with predator confusion, the prey evolved to form linear groups. (**c**) In other runs, here after 1200 generations, the prey evolved to form into tight, rotating circles. The small dots represent the prey and the triangle the predator, with the semicircle showings its visual field. The star indicates where a prey item was captured by the predator (Olson et al. 2013)

travel directions were not strongly aligned. Such prey were more likely to be attacked by the sunfish than were those that were members of coordinated groups. This demonstrates that predators may exert a selective force that favours coordinated, collective movement in prey by disproportionately capturing those that do not exhibit such behaviour. Moreover, the prey do not need to perceive or directly respond to the predators in order for this to occur.

Studies such as these suggest that aggregation and coordinated movement evolve as an effective means of reducing predation risk, albeit perhaps within the context of an evolutionary arms race with predators' ability to effectively track moving, grouped prey. Even relatively simple interaction rules are effective in mitigating predation risk, occurring even without the prey perceiving or directly responding to the predators, and selection may be further maintained by predators disproportionately consuming non-coordinated prey.

10.5 Some Major Consequences Arising from the Transition to Sociality

10.5.1 Selection in Response to Disease and Parasite Exposure

Exposure to pathogens and parasites as a cost of sociality in living group-forming species is discussed in Chaps. 5 and 9. Over evolutionary time, we may expect to see associations between changes in grouping behaviour and exposure to pathogens. In forming groups, animals may be exposed to pathogens and parasites carried by other individuals. Transmission rates may be affected not only through proximity but through interactions such as mating or aggression. Furthermore, some diseases or parasites may flourish when hosts occur in greater densities, meaning that susceptibility to these increases disproportionately in larger groups. Among primates, phylogenetic analysis has revealed that the diversity of parasitic helminths is positively correlated with a number of factors, including body size, diet and also the size of the groups within which they typically live (Vitone et al. 2004). Structures built by groups, such as communal nests or burrows, can also provide niches that viruses, bacteria, fungi and other parasites may adapt to and diversify within and may further drive selection for physiological and behavioural responses that increase immunity (Traniello et al. 2002).

If living in groups increases infection risk, then we may expect to see coevolution between changes in group living and immunity. Such coevolution has been inferred for our own species. Analysis of human genome data has revealed evidence of substantial selection over the last 50 kya. A substantial proportion of this selection, around 10 %, is related to pathogen resistance (Wang et al. 2006). By considering this data alongside archaeological evidence, researchers have reasoned that this selection may have occurred during the transition of societies from hunter-gatherer to agricultural lifestyles. There is evidence for selection for resistance to zoonoses, possibly linked to the domestication of livestock and the adoption of pastoralism. There is also evidence of selection for immunity to so-called crowd diseases, diseases that are more prevalent among larger or denser populations. It is thought that the adoption of agriculture may have led people to settle in centralised communities, living in larger groups and interacting with others to a far greater extent, increasing the carrier reservoirs and the potential for outbreak of such diseases and leading to intensified selection for resistance within agricultural populations (Wang et al. 2006; Laland et al. 2010).

There is evidence that group living has generated selection for mechanisms to reduce the costs of parasite and pathogens in various non-human species too. Eusocial insects, for example, have evolved a range of defences against infection, including adaptive immune responses, antibiotic glandular secretions and behaviours including removal of dead colony members, ejection of diseased individuals and allogrooming (Rosengaus et al. 1998a, b, 2000a, b; Traniello et al. 2002). Allogrooming, removing ectoparasites from others, has evolved in other taxa too. In many species of primates, allogrooming does not function simply as means of reducing parasite loads, it also fulfils important social functions relating to the maintenance of dominance hierarchies, partnerships and coalitions, providing reassurance and reconciliation and in courtship interactions and as a means for instigating copulation (Jolly 1985; Dunbar 1991; Schino 2001). Behaviours that initially functioned to reduce parasite loads then may have been co-opted for use in other contexts, with significant implications for social evolution in those lineages.

10.5.2 Social Cognition

The social brain hypothesis proposes that the interactions between group-living animals form the basis of a selective environment which drives the evolution of brain structure and size and favours particular cognitive capabilities. The brain functions to process information about the environment. Animals that routinely interact with others live in particularly complex social environments; not only do they have to contend with the same problems as animals that are predominantly solitary, such as navigating; finding food, shelter and mates; and avoiding predators and other hazards, they must also overcome the challenges posed by their group mates. These may include recognising individuals, dealing with rivals, competing for status, forming bonds and alliances and even keeping track of the bonds between other group members, reconciling after aggressive interactions and deceiving and manipulating others. As such, the social brain hypothesis predicts that within taxa, particular measures of brain size should be positively correlated with the size and complexity of the groups in which particular species typically live (Byrne and Whiten 1988; Dunbar 1998).

Pérez-Barbería et al. (2007) tested this idea using data on over 200 species of mammal representing three orders: primates, carnivores and ungulates. As a measure of brain size, the authors used the residual of brain size regressed against body size in order to account for the fact that absolute brain size was tightly correlated with body size for the species within their sample. Species that regularly formed associations of two or more adult conspecifics for most of the year were classified as social. For primates, where most species met this criterion, limiting the variation within the sample, they also used a second measure of sociality, the ratio of the geometric mean of each species group size compared to that of all primate species in the sample. Accounting for phylogeny, they found positive correlations between sociality and relative brain size over evolutionary time in each of the three orders. In the case of primates, this relationship was present when sociality was scored using the second metric of sociality, but was absent when the simpler social/nonsocial classification was used. Overall, they argue, their analyses suggest that there has been coevolution between sociality and brain size, supporting the social brain theory.

Another study, by Dunbar and Shultz (2007), compared brain volume (again controlled for body size and phylogeny) between species of ungulates, carnivores, bats, primates and birds that do and do not form pair bonds. For all but the primates, they found that pair-bonding species had greater relative brain volumes than did non-bonding species from within the same order. Pair bonding incorporates cognitively demanding interactions between bonded partners. In the bird, bat, ungulate and carnivore species where it occurs, it is usually seen within the context of reproduction. Dunbar and Shultz argue that there is no difference between pair-bonding and non-pair-bonding anthropoid primate species because the nature of the interactions between all group members is complex, generating similar selective pressures and leading to similar coevolution with brain size as has been seen only between reproductively bonded pairs in the other groups. In other words, they suggest, all members of these primate groups form complex bonds with one another and for functions not only relating to reproduction.

Interestingly, while the social intelligence hypothesis predicts that increasing group size and increasing complexity of social interactions should favour greater investment in the size of the brain or at least in particular regions of it, the distributed cognition hypothesis makes the opposite prediction. Instead of relying upon individual cognition, group members may instead use their many brains to process and communicate information throughout the group. Because such species are able to share the burden of processing information, selection may be expected to favour less and not more investment in costly brain tissue. O’Donnell et al. (2015) tested this idea, comparing the structure of two specific brain regions in nearly 30 wasp species (Vespidae), some of which were solitary and others which were eusocial. They considered two measures of brain morphology, the mean relative sizes of the mushroom body calyces and the antennal to optic lobe ratio. The mushroom body is involved in olfactory learning and memory, while the antennal and optic lobes are involved in peripheral sensory processing. If sociality generates selection upon cognition, then variation in the size of the mushroom bodies may be expected as a function of sociality. Accordingly, O’Donnell and co-workers revealed that investment in mushroom body tissue was lower in social than in solitary species. The antennal to optic lobe ratio, which is not directly associated with memory or learning, was not seen to covary with social structure at all. These findings suggest another route to adapting to a complex social environment: within groups where average relatedness is high and inclusive fitness can be gained through cooperation, it may pay not to invest in energetically costly brain tissue, but instead to rely on collective cognition, distributed among and communicated between group members.

10.5.3 Culture

Animals acquire information from each other, and access to information may be one of the key advantages of group living in many species (see Chap. 4). Such socially transmitted information may relate to day-to-day tasks or problems – the location of food or the appearance of a predator, for example. In other cases, animals may learn from other’s innovations, acquiring new solutions to existing problems or finding out how to solve new ones (Reader and Laland 2003). In other cases still, animals' propensity to use social information over their own personal information may lead to arbitrary behaviours spreading and persisting for some period of time, even across generations, within groups or populations – they may travel again and again to one particular breeding ground, for example, when from an ecological perspective, other grounds that are just as good go unused.

Group- or population-specific behaviours that arise through the use of socially transmitted learning and preferences and which are not entirely due to local ecological conditions or genetic differences between groups have been referred to as traditions or culture. Culture has been defined as group typical patterns of behaviour that are acquired at least in part through socially transmitted information (Laland and Hoppitt 2003; Laland and Janik 2006). It should be noted however that there is substantial debate between researchers over the definition and utility of the concept of culture as applied to non-human animals (Laland and Galef 2009). Terminology aside, group-specific behaviour arising from intra-group social learning is well documented and can have substantial influence over the activities of group members, affecting where they forage, what they feed upon and how they acquire this food. The travelling routes and breeding grounds used by groups can also be affected through such social processes. Examples of naturally occurring or experimentally induced cultures in wild populations are discussed below.

10.5.3.1 Wrasse Breeding Grounds

Bluehead wrasse (*Thalassoma bifasciatum*) use traditional mating sites. The location of these does not appear to reflect local resource distributions. Instead, once established, naïve fish appear to learn their location from experienced members of the population, and their use can persist over many generations. Warner (1988) documented breeding sites that were used on a daily basis over a 12-year period, corresponding to four generations of wrasse. When Warner replaced the entire local population, new fish established breeding sites in different locations, the use of which continued beyond the end of his experiment.

10.5.3.2 Chimpanzee Traditions

Drawing upon data from seven long-term field studies of chimpanzees (*Pan troglodytes*) behaviour, Whiten et al. (1999) described nearly forty behaviours that were found in some populations but which were absent from others, differences which could not be accounted for by variation in the ecological conditions to which the populations were exposed. These included patterns of tool use, specific grooming behaviours and particular courtship interactions. The authors suggest that these represent distinct cultural elements which arise as innovations in certain populations and which subsequently are socially transmitted to others, becoming locally established.

10.5.3.3 Humpback Whale Lob-Tail Feeding

Some members of a population of humpback whales (*Megaptera novaeangliae*) that feeds off the New England coasts uses a particular technique known as lob-tail feeding to capture sand lance (*Ammodytes americanus*). By slapping the surface of the water with their tails, the whales are thought to stun the sand lance, making them easier to capture. This population has been intensively studied for several decades, and lob-tail feeding was seen to dramatically increase in the 1980s. Using social network data, Allen et al. (2013) modelled the spread of this behaviour. Their models suggest that lob-tail feeding is transmitted socially rather than acquired independently, with naïve individuals being more likely to acquire the behaviour if they spend more time associating with others that already performed it. They showed that this behaviour was strongly associated with the presence of sand lance, suggesting that it does indeed have a feeding function. They were also able to rule out the possibility that individuals acquired this behaviour independently but associated with each other because of shared preferences for locations where sand lance were found. Lob-tail feeding has persisted in this population for nearly three decades now and has been transmitted over several generations of whales.

10.5.3.4 Tit Feeder Box Traditions

Aplin et al. (2015) used foraging boxes placed in woodland where they could be accessed by wild great tits to study the spread of artificially seeded local traditions. Many of the great tits living in the area were fitted with tags that could be read by loggers attached to the feeding boxes. The feeding boxes could be accessed in two different ways, and the loggers recorded which of these was used by each tagged bird as it visited the box. The woodland contained several subpopulations of birds. Two birds from each subpopulation were taken into captivity and trained to access the feeding box using one method or the other or else were not trained at all, before being released again. In each subpopulation, naïve birds learned how to access the box, with most of them using the method that was introduced by the trained birds from their area. Most birds persisted in using the seeded method of accessing the box over the alternative. These local biases persisted over two generations. In control subpopulations where the captured birds were not trained to use either method of accessing the feeder box, far fewer birds learned to access it, and those that did were just as likely to use either method. Finally, social network analysis revealed that information was transmitted between birds that frequently associated with one another.

These examples provide evidence of the emergence of cultures in a diverse range of different species. The use of social information is not restricted to group-living species of course (e.g. Lefebvre et al. 1996), but group living may provide a setting in which individuals are routinely exposed to social information, and within which, through process such as convergence and conformity, certain behaviours are promoted more frequently or rewarded more often, leading them to spread and be adopted at a greater rate. Culture then affects the ecology of groups and populations of some species. Whether culture significantly affects fitness or co-evolves with genetic selection in non-human animals, as has been demonstrated in humans (e.g. Beja-Pereira et al. 2003), has yet to be determined.

10.6 Summary

Researchers have addressed the question of the evolution of grouping behaviour from a number of perspectives. Grouping behaviour has been shown to consistently vary between individuals and populations for some species, and it has been established that this behaviour has a heritable component. Translocation experiments have demonstrated that different environments select for grouping to different degrees. Phylogenetic modelling has been used to account for the distribution of grouping and social organisation among extant species (Brashares et al. 2000; Beauchamp 2002; Hughes et al. 2008; Cornwallis et al. 2010; Shultz et al. 2011), while both statistical models informed by phylogenetic relationships, and agent-based simulation models have been valuable in aiding our understanding of the conditions that select for grouping (Olson et al. 2013).

Future developments are likely to centre upon the genetic basis of grouping behaviour and the development and deployment of phylogenetic methods to better understand its evolution. Exciting work with sticklebacks has demonstrated how selection upon both behaviour and perceptory systems shapes shoaling (Greenwood et al. 2013). The combination of rigorous behavioural-genetic approaches along with the declining cost of quantitative trait locus mapping and genotyping and the steady accruement of behavioural and genetic data on model species in open databases should lead to further advances in the genetic underpinnings of social behaviours.

Phylogenetic approaches have proved to be extremely useful in reconstructing the evolution of both group living and cooperative breeding. Such approaches are limited by the accuracy of the phylogenetic trees upon which they are based and by the quality of the data on the traits of interest that are mapped onto these trees, often obtained by meta-analyses of published data sets. We might reasonably expect that the use and accuracy of phylogenetic analyses should increase in the future. First, increasingly sophisticated approaches are allowing researchers to have more confidence in the accuracy of the phylogenetic trees they are able to produce and enabling them to resolve controversial relationships between lineages. Second, the growing culture of open data and the means to curate and share large data sets among interested parties means that the amount of data on behaviour and other traits available for use in such studies grows ever broader and richer.

Conclusions

11

In the preceding chapters, we have reviewed the mechanisms underlying the formation and persistence of animal groups and the functions and trade-offs associated with group living. We have also explored the development and evolution of grouping behaviour. In this final chapter, we summarise the current state of our understanding and, in very broad terms, outline what we consider to be some of the key outstanding questions in each of these four areas.

11.1 Mechanisms

In considering mechanisms, we are concerned both with the interaction rules which determine how animals react to one another as they move though the environment and also the neural and physiological systems which govern how individuals detect, perceive and respond to others that they encounter. Here we consider these separately, although we are aware of course that this distinction can be artificial, for example, with respect to phase changes in locusts (Wang and Kang 2014) or pheromone trail following by ants (Hölldobler and Wilson 1970).

11.1.1 Interaction Rules

The mechanisms behind grouping, coordinated movement and collective decision-making have become a boom area for research over the last two decades. This has not always been the case; despite pioneering early work by the likes of Breder (1951); Radakov (1973) and Reynolds (1987), for a long time functional rather than mechanistic investigations of grouping behaviour dominated. Recent interest has focussed upon simulating the interaction rules governing how individuals respond to their neighbours and the implications of localised interactions for global properties of the group as a whole. Relatively minor differences in attraction and orientation matching between individuals can result in markedly different outcomes for the

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properties of simulated groups, with many of the resulting group configurations closely match those seen in nature, including swarms, polarised schools and revolving tori (Couzin et al. 2002). Other work has focussed upon collective sensing (Berdahl et al. 2013) and mechanisms of decision-making, including the importance of leadership, quorums and consensuses in different systems (Conradt and Roper 2003; Couzin et al. 2005; Ward et al. 2008b).

There are probably a number of reasons for the spike in interest in the mechanisms underlying grouping. One relates to advances in the technology necessary for quantifying movement in large groups of moving animals, for extracting data from videos and tracking devices, and for simulating the movement and implementing the interaction rules between multiple particles and agents. Another stems from the increasing focus upon interdisciplinary collaboration, which has seen biologists, physicists, mathematicians and computer scientists come together to tackle common problems. A third reason is that realistic applications are increasingly being realised for this type of research, from swarm robotics (Şahin 2005) to crowd control solutions (Strömbom et al. 2014).

Collective behaviour is a dynamic and productive area of research. Much of the work in this field is theory driven, and while a great deal of innovative experimental work is being produced, it is probably fair to say that this has not kept pace with theoretical developments. While further experimental work is certainly required, one of the key challenges in this field is to test predictions in nature. This extends to areas including interaction rules, leadership and decision-making and is likely to be aided by developments in tracking and telemetry, which allow for high-resolution data of animal movements (Nagy et al. 2013), and the increasing use of robots and other controllable agents that can be embedded within and interact with members of real groups of animals (Halloy et al. 2007; Faria et al. 2010).

11.1.2 Physiology

Attempts to understand the links between the neural, physiology and hormonal architecture of animals to their behaviour is another burgeoning field of research. Neurological techniques such as electroencephalograms (EEGs) can resolve patterns of the brain/CNS activity with behaviour patterns which may ultimately allow greater insight to the neural underpinnings of aspects of social interactions. Opportunities now exist to study the neural circuitry involved in ever more intricate aspects of social behaviour in increasingly complex animals. Specific disciplines such as electrophysiological olfactography can be used to further appreciate the production, perception and action components of communication between social animals. At present this and similar approaches provide insight to areas such as perception thresholds of cues under clinical conditions. The ability to study the neurological state of free-ranging animals remains some way off; however, this is a tantalising prospect for the future. Meanwhile, collaboration between physiologists and behaviourists continues to shed light on the co-adaptation of metabolism and activity in animals. In the context of social behaviour, this is a hugely promising area; understanding the constraints under which animals operate and the challenges they face allows us to better appreciate their behavioural patterns and strategies. Behavioural endocrinology has provided major insights into relationship between hormones and key aspects of behaviours such as reproduction, aggression and learning. But despite the advances in the above techniques, developing a deep understanding and fully appreciating the links between proximate and ultimate causes of behaviour will be impossible without a much more detailed understanding of the structures and functions of the brain; hence, while progress is impressive, we have some way to go.

11.2 Functions

Animals gain a variety of advantages and pay a range of costs when grouping with others. Common benefits include protection from predators and access to socially transmitted information, while a major cost of grouping is increased competition for resources (Chap. 4). Beyond these, a range of more specific costs and benefits may also apply, depending upon the species and context in question (Chap. 5). Group living then reflects a trade-off between these, and individuals may vary in the extent to which they group with others in response to a range of factors, including their internal state, their perception of the external environment and the threats and resources that it holds. Previous experience, and anticipation of likely future conditions may also shape the tendency of individuals to join groups. While the functions of group living have arguably received the most attention from researchers, compared to mechanisms, development and evolution, there are a number of areas in which key questions remain to be answered.

In Chap. 7, we considered the distribution of different sizes of animal groups, observing that very large groups tend be seen rarely and smaller groups most frequently, with most animals occurring with groups of intermediate size. We noted that while a number of simulation models have been developed that can account for the observed truncated power law distribution of animal group sizes, these models make assumptions about the behaviour of individuals that are not always borne out by experimental findings (Krause and Ruxton 2002). Related to this, the observation that animal group sizes tend to be larger in open versus structured environments has been discussed both in terms of ecological and emergent explanations, which posit different mechanisms (Gerard et al. 2002). Animals may actively form larger groups in the open in order to minimise predation risk, for example. In structured environments, the presence of cover might limit their visibility to predator or provide them with refuge; here larger groups are not necessary in terms of avoiding predators and may even be costly, if they are associated with more intense resource competition or other costs. On the other hand, smaller groups may predominate in structured environments because the presence of cover limits the ability of individuals and smaller groups to detect one another, reducing the rate at which they join up and slowing the rate at which larger groups can form. How groups form and how and why they differ in size between environments are fundamental questions. Here then there is scope for integrating information about group joining biases from studies that consider grouping behaviour at the level of the individual, with modelling approaches that consider the population- or landscape-level processes that lead to the emergence of different group sizes. Similarly, well-designed experiments that are able to distinguish between grouping outcomes that reflect grouping decisions influenced by the external environment and those which arise from limitations on the ability of individuals to detect each other would be valuable.

Group size is also affected by how animals balance the costs and benefits of grouping. When it pays to join others larger or denser groups may be expected, while if grouping is on balance more costly, smaller groups or lone individuals may predominate. This, however, is only part of the story, since the costs and benefits of grouping are rarely likely to apply equally to all members. Individuals are expected to behave selfishly; if it benefits them to join a group, then they should do so, even if their presence reduces the fitness of those already in the aggregation. As a consequence of this, groups are expected to exceed the size at which mean individual fitness is optimised. Incoming individuals should continue to join the group until group size reaches the point at which newcomers would do better if they remained alone. This larger group size is known as the Sibly size after Sibly (1983). Refinements upon this idea have accounted for the ability of individuals or subsets of the group to control resources, thereby influencing the benefit to others of joining or remaining within the group, a branch or research known as skew theory. Some researchers have considered how individuals might proactively recruit or exclude outsiders, while others have incorporated inclusive fitness into their models, in order to make predictions about group sizes under conditions where group members and would-be joiners vary in the degree to which they are related to one another.

Skew theory was developed to capture the conflict between dominants and subordinates over control of limited resources on the one hand and maintaining the stability of the group on the other hand. Here it has been shown that dominants can monopolise resources by punishing or excluding subordinates, but that when it pays to retain subordinates within the group, they can do so by yielding some access to the resource (Vehrencamp 1983; Keller and Reeve 1994). Skew theory has been used to explain the conflicts of interest between cooperative breeders, and much of the empirical research that draws upon it focusses upon such scenarios. More recently, skew theory has been extended to include conflict in other contexts, such as foraging (Hamilton 2000). Social foraging dynamics have received significant attention from theorists and empiricists, and a rich, integrative literature exists on the topic (Giraldeau and Caraco 2000). There is substantial opportunity for further extending skew theory into the domain of social foraging interactions and testing its predictions using some of the many well-established model systems already employed by researchers in this field.

Another area ripe for further research concerns the extension and experimental validation of Sibly's (1983) model to account for the inclusive fitness consequences of group size, as well as the direct gains and costs to the joiner and existing members. Giraldeau and Caraco (1993, 2000) and Higashi and Yamamura (1993) provide models that make testable predictions about the payoffs to the joiner of joining groups composed of kin and non-kin and whether groups should accept or exclude would-be joiners on the basis of their relatedness to them. We predict that kinship may play a more significant role in group joining decisions in species that form stable groups, where relatedness can be determined through kin recognition mechanisms or where high levels of relatedness are statistically probable, as in some cooperative breeders, for example, than in dynamic groups with open entry structure, where individuals frequently mix. In such groups, even though kin recognition between individuals may be possible, we suggest that determining mean relatedness to multiple individuals and where group composition is dynamic may not be possible or at least may incur too wide a margin of error to be a stable strategy. This conjecture, of course, could be confirmed or refuted by formal modelling approaches, and we are also open to the possibility that kin may interact locally, within groups, and that this may affect the fitness of the interactors. One approach to testing such ideas might be to look not at the group as whole but at the role of relatedness in shaping the dyadic interactions that occur within the group, quantifying who associates with, competes with and fights with whom (Croft et al. 2008).

11.3 Development

Developmental effects upon grouping behaviour have been relatively understudied. Sociability changes over the lifetimes of many species (Buske and Gerlai 2011), while early experience can affect the preferences of individuals for grouping with particular phenotypes or even species (Warburton and Lees 1996; Spence and Smith 2007). Giesing et al. (2011) revealed that maternal effects can play a role in shaping grouping behaviour; gravid female sticklebacks that were exposed to predator cues produced young that as juveniles formed denser shoals than did females that were not exposed to predators. Further work into the role of maternal effects upon grouping behaviour in other species would be useful. Female experience might extend to nutritional state and food availability, population density and exposure to different types of predator, all of which might plausibly affect the sociability of offspring. It would be useful to explore the nature and underlying mechanisms of such effects.

The role of embryonic learning, particularly about predators, has been shown to be significant in shaping the subsequent behaviour of juveniles and adults. In some frogs, for example, exposure of embryos to predator odour in conjunction with conspecific injury cues can facilitate learning of novel predators or times of day associated with heighten predation risk in free-swimming tadpoles (Mathis et al. 2008; Ferrari and Chivers 2009). Given that predation is a main driver of grouping in many species, it seems reasonable to predict that exposure to cues indicative of heightened predation risk during embryonic development might also affect sociability subsequently.

11.4 Evolution

Research has established that grouping tendency can vary between individuals and that it has a heritable basis (Chap. 10). Grouping responses are determined by the interaction of genes and other factors such as experience, internal state and environmental conditions. A great deal of progress has been made in this area using relatively few model species. Future work might focus upon establishing a wider range of animal models. Doing so will allow researchers to compare the genetic basis of grouping behaviour and associated neurosensory systems between species and to identify cases of analogous and homologous responses to selection pressures.

Translocation experiments have confirmed that grouping behaviour, along with life history and developmental traits, can indeed evolve in response to environmental conditions. Translocation-type experiments are valuable in that they expose populations to a complex range of natural and often interacting conditions. Such approaches provide powerful tests of the effects of natural selection upon behaviour. There are costs to translocation experiments however. Introduced animals interbreed with resident populations. They may also have effects on local ecology, and once established, they may be impossible to remove. Replicability is also a problem. The famous guppy translocation experiments (Reznick et al. 1990; Magurran 2005) were only performed for two populations in two channels, for example. Mesocosm experiments, in which populations are contained within enclosures, offer a compromise by which some of the costs of translocations can be avoided while still maintaining animals within seminatural conditions. Such an approach also allows for replication. It would be useful to determine whether study populations exposed to the same selection pressures exhibit the same evolutionary responses in terms of grouping and related behaviours.

Advances in phylogenetic analyses have enabled researchers to explore the distribution of grouping behaviour within clades of related species. While earlier analyses took a socioecological approach to understanding the evolution of grouping, attempting to link group size and social structure to ecology, phylogenetic analyses have proved invaluable by allowing the likelihood of convergence (where different species evolve the same response to similar conditions) and constraint (where two or more species or populations exhibit similar behaviour because they are descended from a common ancestor which also displayed this trait) to be determined (Brashares et al. 2000; Shultz et al. 2011). We might expect to gain further insights from such approaches in the future, as more accurate phylogenetic trees are developed and problematic relationships between lineages are resolved and broader and richer behavioural data that can be mapped to them become available. Movement towards a culture of open data means that larger datasets are becoming more readily available to researchers, along with the tools to organise, share and add to them.

11.5 Last Word

Research into the social behaviour of group-living animals has been the main theme of both of our careers to date. In a relatively short time, we have seen transformations in some aspects of this field. Nonetheless, many exciting challenges remain. In this book, we have attempted to provide an integrated summary of the field as it stands, and we have highlighted some of the many ways in which we feel it might develop. We hope that this can form a platform for new and exciting research in the future.

Bibliography

Abbot P, Abe J, Alcock J, Alizon S, Alpedrinha JA, Andersson M, Andre JB, van Baalen M, Balloux F, Balshine S, Barton N, Beukeboom LW, Biernaskie JM, Bilde T, Borgia G, Breed M, Brown S, Bshary R, Buckling A, Burley NT, Burton-Chellew MN, Cant MA, Chapuisat M, Charnov EL, Clutton-Brock T, Cockburn A, Cole BJ, Colegrave N, Cosmides L, Couzin ID, Coyne JA, Creel S, Crespi B, Curry RL, Dall SR, Day T, Dickinson JL, Dugatkin LA, El Mouden C, Emlen ST, Evans J, Ferriere R, Field J, Foitzik S, Foster K, Foster WA, Fox CW, Gadau J, Gandon S, Gardner A, Gardner MG, Getty T, Goodisman MA, Grafen A, Grosberg R, Grozinger CM, Gouyon PH, Gwynne D, Harvey PH, Hatchwell BJ, Heinze J, Helantera H, Helms KR, Hill K, Jiricny N, Johnstone RA, Kacelnik A, Kiers ET, Kokko H, Komdeur J, Korb J, Kronauer D, Kümmerli R, Lehmann L, Linksvayer TA, Lion S, Lyon B, Marshall JA, McElreath R, Michalakis Y, Michod RE, Mock D, Monnin T, Montgomerie R, Moore AJ, Mueller UG, Noë R, Okasha S, Pamilo P, Parker GA, Pedersen JS, Pen I, Pfennig D, Queller DC, Rankin DJ, Reece SE, Reeve HK, Reuter M, Roberts G, Robson SK, Roze D, Rousset F, Rueppell O, Sachs JL, Santorelli L, Schmid-Hempel P, Schwarz MP, Scott-Phillips T, Shellmann-Sherman J, Sherman PW, Shuker DM, Smith J, Spagna JC, Strassmann B, Suarez AV, Sundström L, Taborsky M, Taylor P, Thompson G, Tooby J, Tsutsui ND, Tsuji K, Turillazzi S, Ubeda F, Vargo EL, Voelkl B, Wenseleers T, West SA, West-Eberhard MJ, Westneat DF, Wiernasz DC, Wild G, Wrangham R, Young AJ, Zeh DW, Zeh JA, Zink A (2011) Inclusive fitness theory and eusociality. Nature 471(7339):E1–E4

Abbott KR, Dukas R (2009) Honeybees consider flower danger in their waggle dance. Anim Behav 78(3):633–635

Abrahams MV, Colgan PW (1985) Risk of predation, hydrodynamic efficiency and their influence on school structure. Environ Biol Fishes 13(3):195–202. doi:10.1007/bf00000931

Adamo SA, Hanlon RT (1996) Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? Anim Behav 52:73–81. doi:10.1006/anbe.1996.0153

Adar E, Nottebohm F, Barnea A (2008) The relationship between nature of social change, age, and position of new neurons and their survival in adult zebra finch brain. J Neurosci 28:5394–5400

Agrell J, Wolff JO, Ylönen H (1998) Counter-strategies to infanticide in mammals: costs and consequences. Oikos 83:507–517

Akçay E, Roughgarden J (2007) Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res 9(5):855

Alberts JR (1978) Huddling by rat pups – group behavioral mechanisms of temperature regulation and energy-conservation. J Comp Physiol Psychol 92(2):231–245. doi:10.1037/h0077459

Allen J, Weinrich M, Hoppitt W, Rendell L (2013) Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340(6131):485–488

Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW (1996) Behavior predicts genetic structure in a wild primate group. Proc Natl Acad Sci U S A 93:5797–5801

A. Ward, M. Webster, *Sociality: The Behaviour of Group-Living Animals*,
DOI 10.1007/978-3-319-28585-6

Ame JM, Rivault C, Deneubourg JL (2004) Cockroach aggregation based on strain odour recognition. Anim Behav 68:793–801. doi:10.1016/j.anbehav.2004.01.009

Anacker AMJ, Beery AK (2013) Life in groups: the roles of oxytocin in mammalian sociality. Front Behav Neurosci 7:185

Anderson C (2002) Self-organization in relation to several similar concepts: are the boundaries to self-organization indistinct? Bio B 202(3):247–255. doi:10.2307/1543475

Anderson DJ, Hodum PJ (1993) Predator behavior favors clumped nesting in an oceanic seabird. Ecology 78:2462–2464

Anderson JR, Nilssen AC (1996a) Trapping oestrid parasites of reindeer: the relative age, fat body content and gonotrophic conditions of Cephenemyia trompe and Hypoderma tarandi females caught in baited traps. Med Vet Entomol 10:347–353

Anderson JR, Nilssen AC (1996b) Trapping oestrid parasites of reindeer: the response of Cephenemyia trompe and Hypoderma tarandi to baited traps. Med Vet Entomol 10:337–346

Andrén H (1991) Predation: an overrated factor for over-dispersion of birds' nests? Anim Behav 41(6):1063–1069

Angelier F, Barbraud C, Lormée H, Prud'Homme F, Chastel O (2006) Kidnapping of chicks in emperor penguins: a hormonal by-product? J Exp Biol 209(8):1413–1420

Aoki I (1982) A simulation study on the schooling mechanism in fish. B Jpn Soc Sci Fish 48(8):1081–1088

Aoki I, Inagaki T (1988) Photographic observations on the behavior of Japanese anchovy engraulis-japonica at night in the sea. Mar Ecol Prog Ser 43(3):213–221. doi:10.3354/meps043213

Aparicio JM, Bonal R, Muñoz A (2007) Experimental test on public information use in the colonial lesser kestrel. Evol Ecol 21(6):783–800

Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, Sheldon BC (2013) Individual personalities predict social behaviour in wild networks of great tits (Parus major). Ecol Lett 16(11):1365–1372

Aplin LM, Farine DR, Mann RP, Sheldon BC (2014) Individual-level personality influences social foraging and collective behaviour in wild birds. Pro Roy Soc B Biol Sci 281(1789):20141016

Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518(7540):538–541

Archawaranon M, Dove L, Wiley RH (1991) Social inertia and hormonal-control of aggression and dominance in white-throated sparrows. Behaviour 118:42–65. doi:10.1163/156853991x00193

Arganda S, Perez-Escudero A, de Polavieja GG (2012) A common rule for decision making in animal collectives across species. Proc Natl Acad Sci U S A 109:20508–20513

Armstrong EA, Whitehouse HLK (1977) Behavioral adaptations of wren (troglodytes-troglodytes). Biol Rev Camb Philos Soc 52(2):235–294. doi:10.1111/j.1469-185X.1977.tb01352.x

Arnold KE (2000) Kin recognition in rainbowfish (Melanotaenia eachamensis): sex, sibs and shoaling. Behav Ecol Sociobiol 48(5):385–391

Arnold C, Taborsky B (2010) Social experience in early ontogeny has lasting effects on social skills in cooperatively breeding cichlids. Anim Behav 79:621–630

Arnold SJ, Wassersug RJ (1978) Differential predation on metamorphic anurans by garter snakes (thamnophis) – social-behavior as a possible defense. Ecology 59:1014–1022

Arroyo BE, De Cornulier T, Bretagnolle V (2002) Parental investment and parent–offspring conflicts during the postfledging period in Montagu's harriers. Anim Behav 63(2):235–244

Atema J (1996) Eddy chemotaxis and odor landscapes: exploration of nature with animal sensors. Biol B 191(1):129–138

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432(7013):100–103

Attanasi A, Cavagna A, Del Castello L, Giardina I, Melillo S, Parisi L, Pohl O, Rossaro B, Shen E, Silvestri E, Viale M (2014) Collective behaviour without collective order in wild swarms of midges. Plos Comp Biol 10(7). doi:10.1371/journal.pcbi.1003697

Audubon JJ (1870) The birds of America, from drawings made in the United States and their territories, vol 5. GR Lockwood, Neywork

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, Van Schaik CP (2008) Fission-fusion dynamics new research frameworks. Curr Anthropol 49:627–654

Axelrod R, Hamilton WD (1981) The evolution of cooperation. Science 211(4489):1390–1396

Aycrigg JL, Porter WF (1997) Sociospatial dynamics of white-tailed deer in the central Adirondack Mountains, New York. J Mammal 78:468–482

Baarendse PJJ, Counotte DS, O'Donnell P, Vanderschuren L (2013) Early social experience is critical for the development of cognitive control and dopamine modulation of prefrontal cortex function. Neuropsychopharmacology 38:1485–1494

Baird RW, Dill LM (1996) Ecological and social determinants of group size in transient killer whales. Behav Ecol 7(4):408–416

Bajec IL, Heppner FH (2009) Organized flight in birds. Anim Behav 78(4):777–789. doi:10.1016/j.anbehav.2009.07.007

Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, Orlandi A, Parisi G, Procaccini A, Viale M, Zdravkovic V (2008) Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. Anim Behav 76:201–215. doi:10.1016/j.anbehav.2008.02.004

Balshine-Earn S, Lotem A (1998) Individual recognition in a cooperatively breeding cichlid: evidence from video playback experiments. Behaviour 135:369–386

Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim Behav 29(2):543–550

Bateman AJ (1948) Intra-sexual selection in Drosophila. Heredity 2(Pt. 3):349–368

Bateson PPG (1978a) Sexual imprinting and optimal outbreeding. Nature 273(5664):659–660. doi:10.1038/273659a0

Bateson PPG (1978b) Early experience and sexual preferences. In: Hutchison JB (ed) Biological determinants of sexual behaviour. Wiley, New York, pp 29–53

Bautista A, Garcia-Torres E, Martinez-Gomez M, Hudson R (2008) Do newborn domestic rabbits Oryctolagus cuniculus compete for thermally advantageous positions in the litter huddle? Behav Ecol Sociobiol 62(3):331–339. doi:10.1007/s00265-007-0420-4

Bazazi S, Buhl J, Hale JJ, Anstey ML, Sword GA, Simpson SJ, Couzin ID (2008) Collective motion and cannibalism in locust migratory bands. Curr Biol 18(10):735–739. doi:10.1016/j.cub.2008.04.035

Bazazi S, Ioannou CC, Simpson SJ, Sword GA, Torney CJ, Lorch PD, Couzin ID (2010) The social context of cannibalism in migratory bands of the Mormon Cricket. Plos One 5(12). doi:10.1371/journal.pone.0015118

Beani L, Dallai R, Mercati D, Cappa F, Giusti F, Manfredini F (2011) When a parasite breaks all the rules of a colony: morphology and fate of wasps infected by a strepsipteran endoparasite. Anim Behav 82:1305–1312

Beauchamp G (2002) Higher-level evolution of intraspecific flock-feeding in birds. Behav Ecol Sociobiol 51(5):480–487

Beauchamp G (2008) What is the magnitude of the group-size effect on vigilance? Behav Ecol 19(6):1361–1368

Beauchamp G (2013) Social foragers adopt a riskier foraging mode in the centre of their groups. Biol Lett 9(6):20130528. doi:10.1098/rsbl.2013.0528

Beauchamp G (2014) Social predation: how group living benefits predators and prey. Academic Press, Amsterdam

Beauchamp G, Fernández-Juricic E (2005) The group-size paradox: effects of learning and patch departure rules. Behav Ecol 16(2):352–357

Beauchamp G, Livoreil B (1997) The effect of group size on vigilance and feeding rate in spice finches (Lonchura punctulata). Can J Zool 75(9):1526–1531

Becco C, Vandewalle N, Delcourt J, Poncin P (2006) Experimental evidences of a structural and dynamical transition in fish school. Phy A Stat Mech Appli 367:487–493. doi:10.1016/j.physa.2005.11.041

Beckers R, Deneubourg JL, Goss S (1992a) Trail laying behavior during food recruitment in the ant *Lasius niger* (L). Insect Soc 39(1):59–72. doi:10.1007/bf01240531

Beckers R, Deneubourg JL, Goss S (1992b) Trails and u-turns in the selection of a path by the ant *Lasius niger*. J Theor Biol 159(4):397–415. doi:10.1016/s0022-5193(05)80686-1

Beckers R, Deneubourg JL, Goss S (1993) Modulation of trail laying in the ant lasius-niger (Hymenoptera, Formicidae) and its role in the collective selection of a food source. J Insect Behav 6:751–759

Beckers R, Holland OE, Deneubourg J-L (1994) From local actions to global tasks: Stigmergy and collective robotics. In Brooks R, Maes P (Eds.), Artificial life IV (pp. 181-189). Cambridge, MA: MIT Press

Beecher MD (1989) Signaling systems for individual recognition – an information-theory approach. Anim Behav 38:248–261. doi:10.1016/s0003-3472(89)80087-9

Beecher MD, Beecher IM, Hahn S (1981a) Parent-offspring recognition in bank swallows (Riparia riparia) .2. Development and acoustic basis. Anim Behav 29(FEB):95–101. doi:10.1016/s0003-3472(81)80156-x

Beecher MD, Beecher IM, Lumpkin S (1981b) Parent-offspring recognition in bank swallows (Riparia riparia). 1. Natural history. Anim Behav 29(FEB):86–94. doi:10.1016/s0003-3472(81)80155-8

Beecher MD, Loesche P, Stoddard PK, Medvin MB (1989) Individual recognition by voice in swallows: signal or perceptual adaptation. In: Dooling RJ, Hulse SH (eds) The comparative psychology of audition: perceiving complex sounds. Erlbaum, Hillsdale, pp 227–294

Beehler BM, Foster MS (1988) Hotshots, hotspots, and female preference in the organization of lek mating systems. Am Nat 131:203–219

Beekman M, Fathke RL, Seeley TD (2006) How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? Anim Behav 71:161–171

Beer CG (1970) Individual recognition of voice in the social behaviour of birds. Adv Study Behav 3:27–74

Behringer DC, Butler MJ (2010) Disease avoidance influences shelter use and predation in Caribbean spiny lobster. Behav Ecol Sociobiol 64:747–755

Beja-Pereira A, Luikart G, England PR, Bradley DG, Jann OC, Bertorelle G, Chamberlain AT, Nunes TP, Metodiev S, Ferrand N, Erhardt G (2003) Gene-culture coevolution between cattle milk protein genes and human lactase genes. Nature Gene 35(4):311–313

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. Anim Behav 77(4):771–783

Bennett PM, Owens IP (2002) Evolutionary ecology of birds: life histories, mating systems, and extinction. Oxford University Press, Oxford, pp 1–296

Benoit JB, Del Grosso NA, Yoder JA, Denlinger DL (2007) Resistance to dehydration between bouts of blood feeding in the bed bug, Cimex lectularius, is enhanced by water conservation, aggregation, and quiescence. Am J Trop Med Hyg 76(5):987–993

Berdahl A, Torney CJ, Ioannou CC, Faria JJ, Couzin ID (2013) Emergent Sensing of Complex Environments by Mobile Animal Groups. Science 339(6119):574–576. doi:10.1126/science.1225883

Bergman G, Donner KO (1964) An analysis of the spring migration of the common scoter and the long-tailed duck in southern Finland. Acta Zool Fennica 105:1–59

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank and kinship in baboons. Science 302(5648):1234–1236. doi:10.1126/science.1087513

Bertram BCR (1992) The ostrich communal nesting system. Princeton University Press, Princeton

Biesmeijer JC, Slaa EJ (2004) Information flow and organization of stingless bee foraging. Apidologie 35(2):143–157

Bird CD, Emery NJ (2008) Using video playback to investigate the social preferences of rooks, *Corvus frugilegus*. Anim Behav 76:679–687. doi:10.1016/j.anbehav.2008.04.014

Biro D, Sumpter DJT, Meade J, Guilford T (2006) From compromise to leadership in pigeon homing. Curr Biol 16:2123–2128

Bisazza A, Butterworth B, Piffer L, Bahrami B, Petrazzini MEM, Agrillo C (2014) Collective enhancement of numerical acuity by meritocratic leadership in fish. Sci Rep 4:4560

Bill RG, Herrnkind WF. (1976) Drag reduction by formation movement in spiny lobsters. Science. 193 (4258): 1146–1148.

Black JM (1988) Preflight signaling in swans – a mechanism for group cohesion and flock formation. Ethol 79:143–157

Black JM, Carbone C, Wells RL, Owen M (1992) Foraging dynamics in goose flocks – the cost-of-living on the edge. Anim Behav 44(1):41–50. doi:10.1016/s0003-3472(05)80752-3

Blaustein AR, Waldman B (1992) Kin recognition in anuran amphibians. Anim Behav 44(2):207–221. doi:10.1016/0003-3472(92)90027-7

Bode NWF, Faria JJ, Franks DW, Krause J, Wood AJ (2010) How perceived threat increases synchronization in collectively moving animal groups. Proc Royal Soc B Bio Sci 277(1697):3065–3070. doi:10.1098/rspb.2010.0855

Bode NWF, Wood AJ, Franks DW (2011a) The impact of social networks on animal collective motion. Anim Behav 82(1):29–38. doi:10.1016/j.anbehav.2011.04.011

Bode NWF, Wood AJ, Franks DW (2011b) Social networks and models for collective motion in animals. Behav Ecol Sociobiol 65:117–130. doi:10.1007/s00265-010-1111-0

Boesch C (1994) Cooperative hunting in wild chimpanzees. Anim Behav 48(3):653–667

Boi S, Couzin ID, Del Buono N, Franks NR, Britton NF (1999) Coupled oscillators and activity waves in ant colonies. Proc Royal Soc B Bio Sci 266(1417):371–378

Boinski S, Campbell AF (1995) Use of trill vocalizations to coordinate troop movement among white-faced capuchins – a 2nd field-test. Behaviour 132:875–901

Boissy A, Dumont B (2002) Interactions between social and feeding motivations on the grazing behaviour of herbivores: sheep more easily split into subgroups with familiar peers. App Anim Behav Sci 79(3):233–245. doi:10.1016/s0168-1591(02)00152-1

Bokony V, Lendvai AZ, Liker A (2006) Multiple cues in status signalling: The role of wingbars in aggressive interactions of male house sparrows. Etholo 112(10):947–954. doi:10.1111/j.1439-0310.2006.01246.x

Boland CR (2003) An experimental test of predator detection rates using groups of free-living emus. Ethol 109(3):209–222

Bonabeau E, Dagorn L (1995) Possible universality in the size distribution of fish schools. Phy Rev E 51(6):R5220

Bonabeau E, Theraulaz G, Deneubourg JL, Aron S, Camazine S (1997) Self-organization in social insects. Trends Ecol Evol 12(5):188–193. doi:10.1016/s0169-5347(97)01048-3

Bonabeau E, Dagorn L, Freon P (1999) Scaling in animal group-size distributions. Proc Natl Acad Sci U S A 96:4472–4477

Boogert NJ, Farine DR, Spencer KA (2014) Developmental stress predicts social network position. Biol Lett 10:20140561

Boomsma JJ (2007) Kin selection versus sexual selection: why the ends do not meet. Curr Biol 17(16):R673–R683

Boomsma JJ, Beekman M, Cornwallis CK, Griffin AS, Holman L, Hughes WO, Keller L, Oldroyd BP, Ratnieks FL (2011) Only full-sibling families evolved eusociality. Nature 471(7339):E4–E5

Boratyński JS, Willis CKR, Jefimow M, Wojciechowski MS (2015) Huddling reduces evaporative water loss in torpid Natterer's bats, Myotis nattereri. Comp Biochem Physiol A Mol Integr Phy 179:125–132. doi:http://dx.doi.org/10.1016/j.cbpa.2014.09.035

Borkowski J, Furubayashi K (1998) Seasonal and diel variation in group size among Japanese sika deer in different habitats. J Zool 245(1):29–34

Bosiger YJ, McCormick MI (2014) Temporal links in daily activity patterns between coral reef predators and their prey. Plos One 9(10). doi:10.1371/journal.pone.0111723

Botham MS, Hayward RK, Morrell LJ, Croft DP, Ward JR, Ramnarine I, Krause J (2008) Risk-sensitive antipredator behavior in the Trinidadian guppy, Poecilia reticulata. Ecology 89(11):3174–3185

Boughman JW, Wilkinson GS (1998) Greater spear-nosed bats discriminate group mates by vocalizations. Anim Behav 55:1717–1732. doi:10.1006/anbe.1997.0721

Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Boyd LE (1988) Ontogeny of behavior in Przewalski horses. Appl Anim Behav Sci 21:41–69

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer Associates, Sunderland

Brandl SJ, Bellwood DR (2015) Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes. Sci Rep 5:14556. doi:10.1038/srep14556

Brashares JS, Garland T, Arcese P (2000) Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behav Ecol 11(4):452–463

Breder CM (1951) Studies on the structure of the fish school. B Am Mus Nat Hist 98(1):1–27

Breder CM (1954) Equations descriptive of fish schools and other animal aggregations. Ecology 35(3):361–370. doi:10.2307/1930099

Brennan PL, Prum RO, McCracken KG, Sorenson MD, Wilson RE, Birkhead TR (2007) Coevolution of male and female genital morphology in waterfowl. PLoS One 2(5):e418

Brick O (1998) Fighting behaviour, vigilance and predation risk in the cichlid fish Nannacara anomala. Anim Behav 56(2):309–317

Brierley AS, Cox MJ (2010) Shapes of krill swarms and fish schools emerge as aggregation members avoid predators and access oxygen. Curr Biol 20(19):1758–1762. doi:10.1016/j.cub.2010.08.041

Broly P, Devigne L, Deneubourg JL, Devigne C (2014) Effects of group size on aggregation against desiccation in woodlice (Isopoda: Oniscidea). Physiol Entomol 39(2):165–171. doi:10.1111/phen.12060

Brooke MDL (1985) The effect of allopreening on tick burdens of molting eudyptid penguins. Auk 102:893–895

Brooks R (1999) Mate choice copying in guppies: females avoid the place where they saw courtship. Behaviour 136(4):411–421

Broom M, Ruxton GD (2003) Evolutionarily stable kleptoparasitism: consequences of different prey types. Behav Ecol 14(1):23–33

Brown JL (1975) The evolution of behaviour. Norton, New York

Brown CR (1986) Cliff swallow colonies as information centers. Science 234(4772):83–85

Brown CR, Brown MB (2000) Heritable basis for choice of group size in a colonial bird. Proc Natl Acad Sci 97(26):14825–14830

Brown CR, Brown MB (2004) Empirical measurement of parasite transmission between groups in a colonial bird. Ecology 85(6):1619–1626

Brown SD, Dooling RJ (1992) Perception of conspecific faces by budgerigars (Melopsittacus-undulatus).1. Natural faces. J Comp Psychol 106(3):203–216. doi:10.1037/0735-7036.106.3.203

Brown GE, Godin JGJ, Pedersen J (1999) Fin-flicking behaviour: a visual antipredator alarm signal in a characin fish, Hemigrammus erythrozonus. Anim Behav 58:469–475. doi:10.1006/anbe.1999.1173

Brown C, Garwood MP, Williamson JE (2012) It pays to cheat: tactical deception in a cephalopod social signalling system. Biol Lett 8(5):729–32

Bruce HM (1959) An exteroceptive block to pregnancy in the mouse. Nature 184:105–105

Bruck JN (2013) Decades-long social memory in bottlenose dolphins. Proc R Soc B 280(1768): 20131726. doi:10.1098/rspb.2013.1726

Brunton DH (1997) Impacts of predators: Center nests are less successful than edge nests in a large nesting colony of Least Terns. Condor 99(2):372–380. doi:10.2307/1369943

Bryant DM, Newton AV (1994) Metabolic costs of dominance in dippers, *Cinclus cinclus*. Anim Behav 48(2):447–455. doi:10.1006/anbe.1994.1258

Bshary R, Wickler W, Fricke H (2002) Fish cognition: a primate's eye view. Anim Cogn 5(1):1–13. doi:10.1007/s10071-001-0116-5

Bshary R, Hohner A, Ait-el-Djoudi K, Fricke H (2006) Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. PLoS Biol 4(12):e431. doi:10.1371/journal.pbio.0040431

Buck J, Buck E (1976) Synchronous fireflies. Sci Am 234(5):74–85

Buhl J, Sumpter DJT, Couzin ID, Hale JJ, Despland E, Miller ER, Simpson SJ (2006) From disorder to order in marching locusts. Science 312(5778):1402–1406. doi:10.1126/science.1125142

Buhl J, Sword GA, Clissold FJ, Simpson SJ (2011) Group structure in locust migratory bands. Behav Ecol Sociobiol 65(2):265–273. doi:10.1007/s00265-010-1041-x

Buhl J, Sword GA, Simpson SJ (2012) Using field data to test locust migratory band collective movement models. Interface Focus 2(6):757–763. doi:10.1098/rsfs.2012.0024

Buhrman-Deever SC, Hobson EA, Hobson AD (2008) Individual recognition and selective response to contact calls in foraging brown-throated conures, Aratinga pertinax. Anim Behav 76:1715–1725. doi:10.1016/j.anbehav.2008.08.007

Bull CM, Griffin CL, Lanham EJ, Johnston GR (2000) Recognition of pheromones from group members in a gregarious lizard, Egernia stokesii. J Herpetol 34(1):92–99

Bumann D, Krause J, Rubenstein D (1997) Mortality risk of spatial positions in animal groups: The danger of being in the front. Behaviour 134:1063–1076

Burgerhout E, Tudorache C, Brittijn SA, Palstra AP, Dirks RP, van den Thillart GE (2013) Schooling reduces energy consumption in swimming male European eels, Anguilla anguilla L. J Exp Mar Biol Ecol 448:66–71

Burns ALJ, Herbert-Read JE, Morrell LJ, Ward AJW (2012) Consistency of leadership in Shoals of Mosquitofish (Gambusia holbrooki) in novel and in familiar environments. PLoS One 7(5):e36567. doi:10.1371/journal.pone.0036567

Buske C, Gerlai R (2011) Shoaling develops with age in Zebrafish (Danio rerio). Prog Neuropsychopharmacol Biol Psychiatry 35:1409–1415

Buston P (2003) Forcible eviction and prevention of recruitment in the clown anemonefish. Behav Ecolo 14(4):576–582

Buston PM, Fauvelot C, Wong MYL, Planes S (2009) Genetic relatedness in groups of the humbug damselfish Dascyllus aruanus: small, similar-sized individuals may be close kin. Mol Ecol 18:4707–4715

Butler MJ, MacDiarmid AB, Booth JD (1999) The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. Mar Ecol Prog Ser 188:179–191

Buxton RT, Jones IL (2012) An experimental study of social attraction in two species of storm petrel by acoustic and olfactory cues. Condor 114(4):733–743. doi:10.1525/cond.2012.110091

Byrne RW, Whiten A (1988) Machiavellian Intelligence: social expertise and the evolution of intellect in monkeys apes and humans. Oxford University Press, Oxford

Calabuig G, Ortego J, Aparicio JM, Cordero PJ (2008) Public information in selection of nesting colony by lesser kestrels: which cues are used and when are they obtained? Anim Behav 75(5):1611–1617

Calf K, Adams N, Slotow R (2002) Dominance and huddling behaviour in Bronze Mannikin Lonchura cucullata flocks. Ibis 144(3):488–493. doi:10.1046/j.1474-919X.2002.00039.x

Call J, Aureli F, de Waal FB (1999) Reconciliation patterns among stumptailed macaques: a multivariate approach. Anim Behav 58(1):165–172

Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) Self-organization in biological systems. Princeton University Press, Princeton

Campbell DLM, Hauber ME (2009) Cross-fostering diminishes song discrimination in zebra finches (Taeniopygia guttata). Anim Cogn 12(3):481–490. doi:10.1007/s10071-008-0209-5

Cant MA, Hodge SJ, Bell MB, Gilchrist JS, Nichols HJ (2010) Reproductive control via eviction (but not the threat of eviction) in banded mongooses. Proc Roy Soc B Bio Sci 277(1691): 2219–26

Caraco T, Wolf LL (1975) Ecological determinants of group sizes of foraging lions. Am Nat 109:343–352

Carbone C, Du Toit JT, Gordon IJ (1997) Feeding success in African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group size? J Anim Ecol 66:318–326

Carbone C, Maddox T, Funston PJ, Mills MG, Grether GF, Van Valkenburgh B (2009) Parallels between playbacks and Pleistocene tar seeps suggest sociality in an extinct sabretooth cat, Smilodon. Biol Lett 5(1):81–85

Careau V, Garland T (2015) Energetics and behavior: many paths to understanding. Trends Ecol Evol 30:365–366

Carere C, Drent PJ, Privitera L, Koolhaas JM, Groothuis TG (2005) Personalities in great tits, Parus major: stability and consistency. Anim Behav 70(4):795–805

Carere C, Montanino S, Moreschini F, Zoratto F, Chiarotti F, Santucci D, Alleva E (2009) Aerial flocking patterns of wintering starlings, Sturnus vulgaris, under different predation risk. Anim Behav 77(1):101–107

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago

Carson K, Woodgush DGM (1983) Equine behavior.1. A review of the literature on social and dam foal behavior. App Anim Ethol 10:165–178

Carter GG, Wilkinson GS (2013) Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. Pro Royal Soc Lon B Biol Sci 280(1753):20122573

Carter CS, Grippo AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW (2008) Oxytocin, vasopressin and sociality. Prog Brain Res 170:331–336

Carvalho GR, Shaw PW, Hauser L, Seghers BH, Magurran AE (1996) Artificial introductions, evolutionary change and population differentiation in Trinidadian guppies (Poecilia reticulata: Poeciliidae). Biol J Linn Soc 57(3):219–234

Catterall CP, Kikkawa J, Gray C (1989) Interrelated age-dependent patterns of ecology and behavior in a population of silvereyes (Aves, Zzosteropidae). J Anim Ecol 58:557–570

Chapman CA (1990) Association patterns of spider monkeys – the influence of ecology and sex on social-organization. Behav Ecol Sociobiol 26:409–414

Chapman CA, Lefebvre L (1990) Manipulating foraging group size: spider monkey food calls at fruiting trees. Anim Behav 39(5):891–896

Chapman CA, White FJ, Wrangham RW (1993) Defining subgroup size in fission-fusion societies. Folia Primatol 61:31–34

Chaverri G, Gillam EH, Vonhof MJ (2010) Social calls used by a leaf-roosting bat to signal location. Biol Lett 6(4):441–444. doi:10.1098/rsbl.2009.0964

Cheney DL, Seyfarth RM (1999) Recognition of other individuals' social relationships by female baboons. Anim Behav 58:67–75. doi:10.1006/anbe.1999.1131

Childress MC, Herrnkind WF (1996) The ontogeny of social behavior among juvenile Caribbean spiny lobsters. Anim Behav 51:675–687

Childress MJ, Herrnkind WF (2001) The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. Anim Behav 62:465–472

Chittka L (2004) Dances as windows into insect perception. Plos Biol 2:898–900

Chungu H, Speybroeck N, Pegram RG, Berkvens DL (2001) Rhipicephalus appendiculatus burdens on cattle in relation to age and sex of the host. Tropicultura 19(1):34–36

Clark BR, Faeth SH (1998) The evolution of egg clustering in butterflies: a test of the egg desiccation hypothesis. Evolut Ecol 12(5):543–552

Clark DL, Roberts JA, Uetz GW (2012) Eavesdropping and signal matching in visual courtship displays of spiders. Biol Lett 8:375e378

Clayton NS (1990) The effects of cross-fostering on assortative mating between zebra finch subspecies. Anim Behav 40:1102–1110. doi:10.1016/s0003-3472(05)80176-9

Clutton-Brock T (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296(5565):69–72

Clutton-Brock T, Janson C (2012) Primate socioecology at the crossroads: past, present, and future. Evol Anthropol 21(4):136–150

Clutton-Brock TH, Parker GA (1995) Sexual coercion in animal societies. Anim Behav 49(5):1345–1365

Clutton-Brock TH, Price OF, MacColl AC (1992) Mate retention, harassment, and the evolution of ungulate leks. Behav Ecolo 3(3):234–242

Codling EA, Pitchford JW, Simpson SD (2007) Group navigation and the "many-wrongs principle" in models of animal movement. Ecology 88(7):1864–1870

Cole BJ (1991) Short-term activity cycles in ants – generation of periodicity by worker interaction. Am Nat 137(2):244–259. doi:10.1086/285156

Coleman RA (2010) Limpet aggregation does not alter desiccation in the limpet Cellana tramoserica. J Exp Mar Biol Ecolo 386(1–2):113–118. doi:10.1016/j.jembe.2010.02.011

Collins LM, Sumpter DJT (2007) The feeding dynamics of broiler chickens. J R Soc Interface 4:65–72

Connor RC (1996) Partner preferences in by-product mutualisms and the case of predator inspection in fish. Anim Behav 51(2):451–454

Conradt L (2013) Collective animal decisions: preference conflict and decision accuracy. Inter Focus 3:20130029

Conradt L, List C (2009) Group decisions in humans and animals: a survey. Philos Trans R Soc Lond B Biol Sci 364:719–742

Conradt L, Roper TJ (2000) Activity synchrony and social cohesion: a fission-fusion model. Proc Royal Soc Lon Series B Bio Sci 267:2213–2218

Conradt L, Roper TJ (2003) Group decision-making in animals. Nature 421(6919):155–158

Conradt L, Roper TJ (2005) Consensus decision making in animals. Trends Ecol Evol 20:449–456

Conradt L, Roper TJ (2009) Conflicts of interest and the evolution of decision sharing. Philos Tr Royal Soc B Biol Sci 364(1518):807–819. doi:10.1098/rstb.2008.0257

Conradt L, Krause J, Couzin ID, Roper TJ (2009) “Leading according to need” in self-organizing groups. Am Nat 173:304–312

Conradt L, List C, Roper TJ (2013) Swarm intelligence: when uncertainty meets conflict. Am Nat 182:592–610

Cook M, Mineka S (1989) Observational conditioning of fear to fear-relevant versus fear-irrelevant stimuli in rhesus-monkeys. J Abnorm Psychol 98(4):448–459. doi:10.1037/0021-843x.98.4.448

Coolen I, Giraldeau LA, Lavoie M (2001) Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Anim Behav 61(5):895–903

Coolen I, Bergen YV, Day RL, Laland KN (2003) Species difference in adaptive use of public information in sticklebacks. Pro Royal Soc Lon B Biol Sci 270(1531):2413–2419

Cooper SM (1991) Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. Afr J Ecol 29(2):130–136

Cords M (1995) Predator vigilance costs of allogrooming in wild blue monkeys. Behaviour 132(7):559–569

Cornwallis CK, West SA, Davis KE, Griffin AS (2010) Promiscuity and the evolutionary transition to complex societies. Nature 466(7309):969–972

Costa JT, Gotzek DA, Janzen DH (2003) Late-instar shift in foraging strategy and trail-pheromone use by caterpillars of the neotropical moth Arsenura armida (Cramer) (Saturniidae: Arsenurinae). J Lepidopera Soc 57:220–229

Cote IM, Poulin R (1995) Parasitism and group-size in social animals – a metaanalysis. Behav Ecol 6:159–165

Cote J, Fogarty S, Sih A (2012) Individual sociability and choosiness between shoal types. Anim Behav 83(6):1469–1476

Cotgreave P, Clayton DH (1994) Comparative analysis of time spent grooming by birds in relation to parasite load. Behaviour 131(3):171–187

Cotoneschi C, Dani FR, Cervo R, Sledge MF, Turillazzi S (2007) Polistes dominulus (Hymenoptera : Vespidae) larvae possess their own chemical signatures. J Insect Physiol 53(9):954–963. doi:10.1016/j.jinsphys.2006.12.016

Coulon M, Deputte BL, Heyman Y, Delatouche L, Richard C (2007) Visual discrimination by heifers (Bos taurus) of their own species. J Comp Psychol 121(2):198–204. doi:10.1037/0735-7036.121.2.198

Coulon M, Deputte BL, Heyman Y, Baudoin C (2009) Individual recognition in domestic cattle (Bos taurus): evidence from 2D-images of heads from different breeds. Plos One 4(2). doi:10.1371/journal.pone.0004441

Courtenay SC, Quinn TP, Dupuis HMC, Groot C, Larkin PA (1997) Factors affecting the recognition of population-specific odours by juvenile coho salmon. J Fish Biol 50(5):1042–1060

Courtney SP (1984) The evolution of egg clustering by butterflies and other insects. Am Nat 123:276–281

Couzin ID (2006) Behavioral ecology: social organization in fission-fusion societies. Curr Biol 16:R169–R171

Couzin ID, Franks NR (2003) Self-organized lane formation and optimized traffic flow in army ants. Pro Royal Soc Lon B Biol Sci 270(1511):139–146. doi:10.1098/rspb.2002.2210

Couzin ID, Krause J (2003) Self-organization and collective behavior in vertebrates. In: Advances in the study of behavior, vol 32. pp 1–75

Couzin ID, Krause J, James R, Ruxton GD, Franks NR (2002) Collective memory and spatial sorting in animal groups. J Theor Biol 218(1):1–11. doi:10.1006/yjtbi.3065

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433(7025):513–516. doi:10.1038/nature03236

Couzin ID, Ioannou CC, Demirel G, Gross T, Torney CJ, Hartnett A, Conradt L, Levin SA, Leonard NE (2011) Uninformed individuals promote democratic consensus in animal groups. Science 334:1578–1580

Cox MD, Blanchard GB (2000) Gaseous templates in ant nests. J Theor Biol 204(2):223–238. doi:10.1006/jtbi.2000.2010

Cozzie LR, Irby WS (2010) Anti-insect defensive behaviors in equines post-West Nile virus infection. J Veterinary Beha Clini Appl Res 5:13–21

Creel, S (2001) Social dominance and stress hormones. Trends in Ecology & Evolution , Volume 16 , Issue 9 , 491–497

Creel S, Creel NM (1995) Communal hunting and pack size in African wild dogs, Lycaon pictus. Anim Behav 50(5):1325–1339

Creel S, Schuette P, Christianson D (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behav Ecolo 25(4):773–784

Cresswell W (1997) Interference competition at low competitor densities in blackbirds Turdus merula. J Anim Ecol 66:461–471

Cresswell W (1998) Variation in the strength of interference competition with resource density in blackbirds Turdus merula. Oikos 81:152–160

Croft DP, Arrowsmith BJ, Bielby J, Skinner K, White E, Couzin ID, Magurran IR, Krause J (2003) Mechanisms underlying shoal composition in the Trinidadian guppy, Poecilia reticulata. Oikos 100(3):429–438

Croft DP, James R, Ward AJW, Botham MS, Mawdsley D, Krause J (2005) Assortative interactions and social networks in fish. Oecologia 143:211–219

Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton University Press, Princeton

Croft DP, Darden SK, Ruxton GD (2009a) Predation risk as a driving force for phenotypic assortment: a cross-population comparison. Proc Roy Soc B 276(1663):1899–904

Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R (2009b) Behavioural trait assortment in a social network: patterns and implications. Behav Ecol Sociobiol 63(10):1495–1503

Croft DP, Edenbrow M, Darden SK, Ramnarine IW, van Oosterhout C, Cable J (2011) Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies Poecilia reticulata. Behav Ecol Sociobiol 65:2219–2227

Crofton HD (1958) Nematode parasite populations in sheep on lowland farms.6. sheep behaviour and nematode infections. Parasitology 48(3–4):251–260

Crook JH, Gartlan JS (1966) Evolution of primate societies. Nature 210(5042):1200

Cross PC, Lloyd-Smith JO, Bowers JA, Hay CT, Hofmeyr M, Getz WM (2004) Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. Ann Zoologici Fennici 41:879–892

Cross PC, Lloyd-Smith JO, Getz WM (2005) Disentangling association patterns in fission-fusion societies using African buffalo as an example. Anim Behav 69:499–506

Croxall JP, Silk JR, Phillips RA, Afanasyev V, Briggs DR (2005) Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. Science 307(5707):249–250

Cullen JM, Shaw E, Baldwin HA (1965) Methods for measuring 3-dimensional structure of fish schools. Animal Behaviour 13(4):534. doi:10.1016/0003-3472(65)90117-x

Cvikel N, Berg KE, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y (2015) Bats aggregate to improve prey search but might be impaired when their density becomes too high. Curr Biol 25(2):206–211

Czirok A, Vicsek T (2000) Collective behavior of interacting self-propelled particles. Phys A Stat Mech Appl 281(1–4):17–29. doi:10.1016/s0378-4371(00)00013-3

Czirok A, Vicsek M, Vicsek T (1999) Collective motion of organisms in three dimensions. Phys A Stat Mech Appl 264(1–2):299–304. doi:10.1016/s0378-4371(98)00468-3

D'Eath RB, Stone RJ (1999) Chickens use visual cues in social discrimination: an experiment with coloured lighting. Appl Anim Behav Sci 62(2–3):233–242. doi:10.1016/s0168-1591(98)00216-0

D'Ettorre P, Heinze J (2001) Sociobiology of slave-making ants. Acta Etholo 3(2):67–82

da Costa AP, Leigh AE, Man MS, Kendrick KM (2004) Face pictures reduce behavioural, autonomic, endocrine and neural indices of stress and fear in sheep. Proc Royal Soc B Biol Sci 271(1552):2077–2084. doi:10.1098/rspb.2004.2831

Dale J, Lank DB, Reeve HK (2001) Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. Am Nat 158(1):75–86. doi:10.1086/320861

Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20:187–193

Danchin E, Wagner RH (1997) The evolution of coloniality: the emergence of new perspectives. Trends Ecol Evol 12:342–347

Danchin É, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. Science 305(5683):487–491

Darden SK, Croft DP (2008). Male harassment drives females to alter habitat use and leads to segregation of the sexes. Biology letters, 4(5), 449–451.

Darden SK, James R, Ramnarine IW, Croft DP (2009). Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. Proceedings of the Royal Society of London B: Biological Sciences, 276(1667), 2651–2656.

Davenport D, Norris KS (1958) Observations on the symbiosis of the sea anemone stoichactis and the pomacentrid fish, *Amphiprion percula*. Biol B 115(3):397–410. doi:10.2307/1539105

Davies NB, Krebs JR, West SA (2012) An introduction to behavioural ecology. Wiley, Oxford

Davis JM (1975) Socially induced flight reactions in pigeons. Animal Behaviour 23:597

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

de Waal F (1982) Chimpanzee politics. Power and sex among apes. Chimpanzee politics. Power and sex among apes. The John Hopkins University Press, Baltimore, Maryland

DeBlois EM, Rose GA (1996) Cross-shoal variability in the feeding habits of migrating Atlantic cod (Gadus morhua). Oecologia 108(1):192–196

Delestrade A (1994) Factors affecting flock size in the alpine chough pyrrhocorax-graculus. Ibis 136:91–96

Dell AI, Bender JA, Branson K, Couzin ID, de Polavieja GG, Noldus L, Perez-Escudero A, Perona P, Straw AD, Wikelski M, Brose U (2014) Automated image-based tracking and its application in ecology. Trends Ecol Evol 29(7):417–428. doi:10.1016/j.tree.2014.05.004

Dell'Ariccia G, Dell'Omo G, Wolfer DP, Lipp HP (2008) Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. Anim Behav 76:1165–1172

Delville Y, David JT, Taravosh-Lahn K, Wommack JC (2003) Stress and the development of agonistic behavior in golden hamsters. Horm Behav 44:263–270

Deneubourg JL, Goss S (1989) Collective patterns and decision-making. Etholo Ecolo Evol 1:295–311

Deneubourg JL, Lioni A, Detrain C (2002) Dynamics of aggregation and emergence of cooperation. Biol B 202:262–267

Despland E, Hamzeh S (2004) Ontogenetic changes in social behaviour in the forest tent caterpillar, Malacosoma disstria. Behav Ecol Sociobiol 56:177–184

Desrochers A (1989) Sex, dominance, and microhabitat use in wintering black-capped chickadees – a field experiment. Ecology 70(3):636–645. doi:10.2307/1940215

Detto T, Backwell PRY, Hemmi JM, Zeil J (2006) Visually mediated species and neighbour recognition in fiddler crabs (Uca mjoebergi and Uca capricomis). Proc Royal Soc B Biol Sci 273(1594):1661–1666. doi:10.1098/rspb.2006.3503

Deutsch A, Theraulaz G, Vicsek T (2012) Collective motion in biological systems. Interface Focus 2(6):689–692. doi:10.1098/rsfs.2012.0048

Devito J, Chivers DP, Kiesecker JM, Marco A, Wildy EL, Blaustein AR (1998) The effects of snake predation on metamorphosis of western toads, Bufo boreas (Amphibia, Bufonidae). Etholo 104(3):185–193

Di Bitetti MS, Janson CH (2001) Social foraging and the finder's share in capuchin monkeys, Cebus apella. Anim Behav 62(1):47–56

Di Blanco Y, Hirsch BT (2006) Determinants of vigilance behavior in the ring-tailed coati (Nasua nasua): the importance of within-group spatial position. Behav Ecol Sociobiol 61(2):173–182. doi:10.1007/s00265-006-0248-3

Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci 91(21):9941–9945

Dill LM, Dunbrack RL, Major PF (1981) A new stereophotographic technique for analyzing the three-dimensional structure of fish schools. Environ Biol Fishes 6:7–13

Dingemanse NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. Proc Royal Soc London Series B Biol Sci 271(1541): 847–852

Dittrich W (1990) Representation of faces in longtailed macaques (*Macaca fascicularis*). Etholo 85(4):265–278

Dittus WP (1988) Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. Anim Behav 36(6):1626–1645

Dobler R, Kölliker M (2010) Kin-selected siblicide and cannibalism in the European earwig. Behav Ecolo 21(2):257–263

Dolby AS, Grubb TC Jr (1998) Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Anim Behav 56(2):501–509

Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. Science 297(5584):1168–1170

Domenici P, Lefrancois C, Shingles A (2007) Hypoxia and the antipredator behaviours of fishes. Philos Trans R Soc Lond B Biol Sci 362(1487):2105–2121

Doonan IJ, Bull B, Coombs RF (2003) Star acoustic surveys of localized fish aggregations. Ices J Marine Sci 60(1):132–146. doi:10.1006/jmsc.2002.1331

Dorigo M, Stutzle T (2004) Ant colony optimization. MIT Press, Cambridge

Dorigo M, Maniezzo V, Colorni A (1996) Ant system: optimization by a colony of cooperating agents. IEEE Trans Syst Man Cybern B Cybern 26(1):29–41. doi:10.1109/3477.484436

Dornhaus A, Chittka L (2004) Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.). Apidologie 35:183–192

Dornhaus A, Powell S, Bengston S (2012) Group size and its effects on collective organization. Annu Rev Entomol 57(57):123–141

Drea CM, Vignieri SN, Kim HS, Weldele ML, Glickman SE (2002) Responses to olfactory stimuli in spotted hyenas (crocuta crocuta): II. Discrimination of conspecific scent. J Comp Psychol 116(4):342–349. doi:10.1037//0735-7036.116.4.342

Duffy DC (1983) The foraging ecology of Peruvian seabirds. Auk 800–810

Dugatkin LA (1988) Do guppies play tit for tat during predator inspection visits? Behav Ecol Sociobiol 23(6):395–399

Dugatkin LA, Alfieri M (1991) Guppies and the TIT FOR TAT strategy: preference based on past interaction. Behav Ecol Sociobiol 28(4):243–246

Dugatkin LA, Godin JGJ (1993) Female mate copying in the guppy (Poecilia reticulata): age-dependent effects. Behav Ecolo 4(4):289–292

Dugatkin LA, Fitzgerald GJ, Lavoie J (1994) Juvenile 3-spined sticklebacks avoid parasitized conspecifics. Environ Biol Fishes 39:215–218

Duijns S, Piersma T (2014) Interference competition in a sexually dimorphic shorebird: prey behaviour explains intraspecific competition. Anim Behav 92:195–201

Dukas R (2002) Behavioural and ecological consequences of limited attention. Philos Tr Royal Soc B Biol Sci 357:1539–1547

Dukas R, Kamil A (2000) The cost of limited attention in blue jays. Behav Ecolo 11:502–506

Dunbar RI (1991) Functional significance of social grooming in primates. Folia Primatol 57(3):121–131

Dunbar RIM (1998) The social brain hypothesis. Evol Anthropol 6:178–190

Dunbar R, Dunbar P (1975) Social dynamics of gelada baboons. Contrib Primatol 6:1–157

Dunbar RIM, Shultz S (2007) Evolution in the social brain. Science 317:1344–1347

Dussutour A, Simpson SJ, Despland E, Colasurdo N (2007) When the group denies individual nutritional wisdom. Anim Behav 74:931–939

Duvall D (1986) A new question of pheromones: aspects of possible chemical signaling and reception in the mammal-like reptiles. In: Hotton N, MacLean PD, Roth JJ, Roth EC (eds) The ecology and biology of mammal-like reptiles. Smithsonian Institution Press, Washington, DC, pp 219–238

Dyer JRG, Croft DP, Morrell LJ, Krause J (2008) Shoal composition determines foraging success in the guppy. Behav Ecolo 20:165–171

Dzieweczynski TL, Crovo JA (2011) Shyness and boldness differences across contexts in juvenile three spined stickleback *Gasterosteus aculeatus* from an anadromous population. J Fish Biol 79(3):776–788

Ebensperger LA (2001) A review of the evolutionary causes of rodent group-living. Acta Theriol 46(2):115–144

Edelman AJ, Koprowski JL (2007) Communal nesting in asocial Abert's squirrels: the role of social thermoregulation and breeding strategy. Etholo 113(2):147–154

Edwards DH, Kravitz EA (1997) Serotonin, social status and aggression. Curr Opin Neurobiol 7:812–819

Eens M, Van Duyse E, Berghman L, Pinxten R (2000) Shield characteristics are testosterone-dependent in both male and female moorhens. Horm Behav 37(2):126–134. doi:10.1006/hbeh.1999.1569

Einon DF, Morgan MJ (1977) Critical period for social-isolation in rat. Dev Psychobiol 10:123–132

Ekman J (1986) Tree use and predator vulnerability of wintering passerines. Ornis Scan 17(3):261–267. doi:10.2307/3676836

Ekman J (1987) Exposure and time use in willow tit flocks – the cost of subordination. Anim Behav 35:445–452. doi:10.1016/s0003-3472(87)80269-5

Ekman JB, Askenmo CEH (1984) Social rank and habitat use in willow TIT groups. Anim Behav 32(MAY):508–514. doi:10.1016/s0003-3472(84)80288-2

Elekonich MM, Wingfield JC (2000) Seasonality and hormonal control of territorial aggression in female song sparrows (Passeriformes: Emberizidae: Melospiza melodia). Etholo 106:493–510

Elliott JM (2002) Shadow competition in wild juvenile sea trout. J Fish Biol 61(5):1268–1281

Emery AR (1973) Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J Fish Res Board Can 30(6):761–775

Emlen ST (1984) Cooperative breeding in birds and mammals. In Behavioural ecology: an evolutionary approach (eds. Krebs JR, Davies NB), pp. 305–339. Sunderland, MA: Sinauer

Engelhardt SC, Weladji RB, Holand Ø, Røed KH, Nieminen M (2015) Evidence of reciprocal allonursing in reindeer, rangifer tarandus. Ethology, 121:245–259. doi: 10.1111/eth.12334

Engeszer RE, Ryan MJ, Parichy DM (2004) Learned social preference in zebrafish. Curr Biol 14:881–884

Erhart EM, Overdorff DJ (1999) Female coordination of group travel in wild Propithecus and Eulemur. Int J Primatol 20:927–940

Eriksson A, Jacobi MN, Nystrom J, Tunstrom K (2010) Determining interaction rules in animal swarms. Behav Ecology 21(5):1106–1111. doi:10.1093/beheco/arq118

Estes R (1991) The behavior guide to African mammals, vol 64. University of California Press, Berkeley

Evans RM (1982) Foraging-flock recruitment at a black-billed gull colony: implications for the information center hypothesis. Auk 99:24–30

Evans SR, Finnie M, Manica A (2007) Shoaling preferences in decapod crustacea. Anim Behav 74:1691–1696. doi:10.1016/j.anbehav.2007.03.017

Evershed RP, Morgan ED, Cammaerts MC (1982) 3-ethyl-2,5-dimethylpyrazine, the trail pheromone from the venom gland of 8 species of myrmica ants. Insect Biochem 12(4):383–391. doi:10.1016/0020-1790(82)90035-x

Ewer RF (1973) The carnivores. Cornell University Press, Ithaca

Fairbanks LA (1993) Risk-taking by juvenile vervet monkeys. Behaviour 124:57–72

Falls JB, Krebs JR, McGregor PK (1982) Song matching in the great tit (parus-major) – the effect of similarity and familiarity. Anim Behav 30(NOV):997–1009. doi:10.1016/s0003-3472(82)80188-7

Faria JJ, Dyer JR, Clément RO, Couzin ID, Holt N, Ward AJW, Water D, Krause J (2010) A novel method for investigating the collective behaviour of fish: introducing 'Robofish'. Behav Ecol Sociobiol 64(8):1211–1218

Farine DR, Garroway CJ, Sheldon BC (2012) Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. Anim Behav 84(5):1271–1277

Fauchald P, Rodven R, Bardsen BJ, Langeland K, Tveraa T, Yoccoz NG, Ims RA (2007) Escaping parasitism in the selfish herd: age, size and density-dependent warble fly infestation in reindeer. Oikos 116:491–499

Feare CJ (1976) Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus-infested ticks. Ibis 118:112–115

Feeney WE, Medina I, Somveille M, Heinsohn R, Hall ML, Mulder RA, Stein JA, Kilner RM, Langmore NE (2013) Brood parasitism and the evolution of cooperative breeding in birds. Science 342(6165):1506–1508

Ferrari MC, Chivers DP (2009) Temporal variability, threat sensitivity and conflicting information about the nature of risk: understanding the dynamics of tadpole antipredator behaviour. Anim Behav 78(1):11–16

Ferrari MC, Chivers DP (2010) The ghost of predation future: threat-sensitive and temporal assessment of risk by embryonic woodfrogs. Behav Ecol Sociobiol 64(4):549–555

Fischer S, Bessert-Nettelbeck M, Kotrschal A, Taborsky B (2015) Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. Am Natu 186:123–140

Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier MJ, Rubenstein DI (2007) Social relationships and reproductive state influence leadership roles in movements of plains zebra, Equus burchellii. Anim Behav 73:825–831

Fish FE (1995) Kinematics of ducklings swimming in formation – consequences of position. J Exper Zoo 273(1):1–11. doi:10.1002/jez.1402730102

Fish FE (2010) Swimming strategies for energy economy. In: Domenici P, Kapoor BG (eds) Fish swimming: an etho-ecological perspective. Science Publishers, Enfield, pp 90–122

Fiske P, Rintamäki PT, Karvonen E (1998) Mating success in lekking males: a meta-analysis. Behav Ecolo 9(4):328–338

Fitzgerald TD (1993) Sociality in caterpillars. In: Stamp N, Casey T (eds) Caterpillars: ecological and evolutionary constraints on foraging. Chapman and Hall, New York, pp 372–403

Fitzgibbon CD (1990) Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Anim Behav 39(6):1116–1126

FitzGibbon CD (1994) The costs and benefits of predator inspection behaviour in Thomson's gazelles. Behav Ecol Sociobiol 34(2):139–148

Flack A, Pettit B, Freeman R, Guilford T, Biro D (2012) What are leaders made of? The role of individual experience in determining leader-follower relations in homing pigeons. Anim Behav 83:703–709

Fletcher RJ Jr (2009) Does attraction to conspecifics explain the patch-size effect? An experimental test. Oikos 118(8):1139–1147. doi:10.1111/j.1600-0706.2009.17342.x

Fletcher DJC, Michener CD (1987) Kin recognition in animals. John Wiley, New York

Flierl G, Grunbaum D, Levin S, Olson D (1999) From individuals to aggregations: the interplay between behavior and physics. J Theor Biol 196(4):397–454

Fone KCF, Porkess MV (2008) Behavioural and neurochemical effects of post-weaning social isolation in rodents – relevance to developmental neuropsychiatric disorders. Neurosci Biobehav Rev 32:1087–1102

Foster SA (1985) Group foraging by a coral-reef fish – a mechanism for gaining access to defended resources. Anim Behav 33(AUG):782–792

Foster EA, Franks DW, Mazzi S, Darden SK, Balcomb KC, Ford JKB, Croft DP (2012) Adaptive prolonged postreproductive life span in killer whales. Science 337(6100):1313. doi:10.1126/science.1224198

Fowler CD, Liu Y, Ouimet C, Wang Z (2002) The effects of social environment on adult neurogenesis in the female prairie vole. J Neurobiol 51:115–128

Fox MW (1972) Behavior of wolves, dogs, and related canids. Harper and Row, New York

Frank LG (1986) Social-organization of the spotted hyena Crocuta crocuta.2. Dominance and reproduction. Anim Behav 34:1510–1527. doi:10.1016/s0003-3472(86)80221-4

Franks NR (1985) Reproduction, foraging efficiency and worker polymorphism in army ants. Fortschritte Der Zoologie 31:91–107

Franks NR, Bryant S (1987) Rhythmical patterns of activity within the nest of ants. In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Peperny, Munich

Franks NR, Richardson T (2006) Teaching in tandem-running ants. Nature 439:153

Franks NR, Dornhaus A, Fitzsimmons JP, Stevens M (2003a) Speed versus accuracy in collective decision making. Proce Royal Soc London Series B Biol Sci 270:2457–2463

Franks NR, Mallon EB, Bray HE, Hamilton MJ, Mischler TC (2003b) Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. Anim Behav 65:215–223

Franks NR, Hooper J, Webb C, Dornhaus A (2005) Tomb evaders: house-hunting hygiene in ants. Biol Lett 1:190–192

Franks NR, Dornhaus A, Metherell BG, Nelson TR, Lanfear SAJ, Symes WS (2006) Not everything that counts can be counted: ants use multiple metrics for a single nest trait. Proce Royal Soc London Series B Biolo Sci 273:165–169

Franks NR, Dornhaus A, Hitchcock G, Guillem R, Hooper J, Webb C (2007) Avoidance of conspecific colonies during nest choice by ants. Anim Behav 73:525–534

Franks NR, Dechaume-Moncharmont FX, Hanmore E, Reynolds JK (2009) Speed versus accuracy in decision-making ants: expediting politics and policy implementation. Philos T Royal Soc B Biol Sci 364:845–852

Freeberg TM, Lucas JR (2002) Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees *Poecile carolinensis*. Anim Behav 63(5):837–845

Fretwell SD (1972) Populations in a seasonal environment (No. 5). Princeton University Press, Princeton, NJ, USA

Fricke HW (1973) Individual partner recognition in fish – field studies on *Amphiprion bicinctus*. Naturwissenschaften 60(4):204–205

Frommen JG, Mehlis M, Brendler C, Bakker TCM (2007) Shoaling decisions in three-spined sticklebacks (Gasterosteus aculeatus) – familiarity, kinship and inbreeding. Behav Ecolo Soc 61(4):533–539. doi:10.1007/s00265-006-0281-2

Frommolt KH, Goltsman ME, MacDonald DW (2003) Barking foxes, Alopex lagopus: field experiments in individual recognition in a territorial mammal. Anim Behav 65:509–518. doi:10.1006/anbe.2003.2064

Fuiman LA, Magurran AE (1994) Development of predator defenses in fishes. Rev Fish Biol Fisher 4:145–183

Furmankiewicz J, Ruczynski I, Urban R, Jones G (2011) Social calls provide tree-dwelling bats with information about the location of conspecifics at roosts. Etholo 117(6):480–489. doi:10.1111/j.1439-0310.2011.01897.x

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655–656

Gagliardo A, Guilford T (1993) Why do warning-coloured prey live gregariously? Proce Royal Soc London Series B Biol Sci 251(1330):69–74

Gaioni SJ, Ross LE (1982) Distress calling induced by reductions in group-size in ducklings reared with conspecifics or imprinting stimuli. Anim Learn Behav 10(4):521–529. doi:10.3758/bf03212294

Galef BG (1988) Imitation in animals: history, definition and interpretation of the data from the psychological laboratory. In: Galef BG, Zentall TR (eds) Social learning: psychological and biological perspectives. Erlbaum, Hillsdale

Galef BG (1996) Social enhancement of food preferences in Norway rats: a brief review. In: Heyes CM, Galef BG (eds) Social learning in animals: the roots of culture. Academic Press, San Diego, pp 49–64

Galef BG (2009) Strategies for social learning: testing predictions from formal theory. Adv Study Behav 39:117–151

Galef BG, Buckley LL (1996) Use of foraging trails by Norway rats. Anim Behav 51:765–771

Galef BG, White DJ (1997) Socially acquired information reduces Norway rats' latencies to find food. Anim Behav 54:705–714

Galef BG, Wigmore SW (1983) Transfer of information concerning distant foods: a laboratory investigation of the 'information-centre'hypothesis. Anim Behav 31(3):748–758

Galton F (1907) Vox populi. Nature 75:450–451

Gamboa GJ, Reeve HK, Ferguson ID, Wacker TL (1986) Nestmate recognition in social wasps – the origin and acquisition of recognition odors. Anim Behav 34:685–695. doi:10.1016/s0003-3472(86)80053-7

Gandon S (1999) Kin competition, the cost of inbreeding and the evolution of dispersal. J Theor Biol 200(4):345–364

Gautrais J, Ginelli F, Fournier R, Blanco S, Soria M, Chate H, Theraulaz G (2012) Deciphering interactions in moving animal groups. Plos Compu Biol 8(9). doi:10.1371/journal.pcbi.1002678

Gerard JF, Loisel P (1995) Spontaneous emergence of a relationship between habitat openness and mean group size and its possible evolutionary consequences in large herbivores. J Theor Biol 176(4):511–522

Gerard JF, Bideau E, Maublanc ML, Loisel P, Marchal C (2002) Herd size in large herbivores: encoded in the individual or emergent? Biol Bull 202(3):275–282

Gerlach G, Lysiak N (2006) Kin recognition and inbreeding avoidance in zebrafish, Danio rerio, is based on phenotype matching. Anim Behav 71:1371–1377. doi:10.1016/j.anbehav.2005.10.010

Gerlach G, Hodgins-Davis A, Avolio C, Schunter C (2008) Kin recognition in zebrafish: a 24-hour window for olfactory imprinting. Proce Royal Soc London Series B Biol Sci 275(1647):2165–2170. doi:10.1098/rspb.2008.0647

Gherardi F, Tricarico E, Atema J (2005) Unraveling the nature of individual recognition by odor in hermit crabs. J Chem Ecol 31(12):2877–2896. doi:10.1007/s10886-005-8400-5

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15(5):745–762. doi:10.1007/s10071-012-0513-y

Gheusi G, Bluthe RM, Goodall G, Dantzer R (1994) Social and individual recognition in rodents – methodological aspects and neurobiological bases. Behav Processes 33(1–2):59–87. doi:10.1016/0376-6357(94)90060-4

Giesing ER, Suski CD, Warner RE, Bell AM (2011) Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. Proc Royal Soc B Biol Sci 278:1753–1759

Gilbert C, Robertson G, Le Maho Y, Naito Y, Ancel A (2006) Huddling behavior in emperor penguins: dynamics of huddling. Physiol Behav 88(4–5):479–488. doi:10.1016/j.physbeh.2006.04.024

Gilbert C, McCafferty D, Le Maho Y, Martrette JM, Giroud S, Blanc S, Ancel A (2010) One for all and all for one: the energetic benefits of huddling in endotherms. Biol Rev 85(3):545–569. doi:10.1111/j.1469-185X.2009.00115.x

Giraldeau LA, Caraco T (1993) Genetic relatedness and group size in an aggregation economy. Evol Ecol 7(4):429–438

Giraldeau L-A, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton

Giraldeau LA, Gillis D (1985) Optimal group size can be stable: a reply to Sibly. Anim Behav 33(2):666–667

Giraldeau LA, Lefebvre L (1986) Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. Anim Behav 34(3):797–803

Giraldeau LA, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. Philosophical transactions of the Royal Society of London. Series B Biol Sci 357(1427):1559–1566

Godin J-GJ, Morgan MJ (1985) Predator avoidance and school size in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus* Lesueur). Behav Ecol Sociobiol 16:105–110

Godin J-GJ, Herdman EJ, Dugatkin LA (2005) Social influences on female mate choice in the guppy, Poecilia reticulata: generalized and repeatable trait-copying behaviour. Anim Behav 69(4):999–1005

Goles E, Schulz O, Markus M (2001) Prime number selection of cycles in a predator prey model. Complexit 6(4):33–38

Gonda A, Herczeg G, Merila J (2009) Habitat-dependent and -independent plastic responses to social environment in the nine-spined stickleback (Pungitius pungitius) brain. Proce Royal Soc London Series B Biol Sci 276:2085–2092

Goodale E, Ratnayake CP, Kotagama SW (2014) Vocal mimicry of alarm associated sounds by a drongo elicits flee and mobbing responses from other species that participate in mixed species bird flocks. Etholo 120(3):266–274

Goodson JL (1998a) Territorial aggression and dawn song are modulated by septal vasotocin and vasoactive intestinal polypeptide in male field sparrows (Spizella pusilla). Horm Behav 34:67–77

Goodson JL (1998b) Vasotocin and vasoactive intestinal polypeptide modulate aggression in a territorial songbird, the violet-eared waxbill (Estrildidae: Uraeginthus granatina). Gen Comp Endocrinol 111:233–244

Goodson JL, Adkins-Regan E (1999) Effect of intraseptal vasotocin and vasoactive intestinal polypeptide infusions on courtship song and aggression in the male zebra finch (Taeniopygia guttata). J Neuroendocrinol 11:19–25

Goodson JL, Schrock SE, Klatt JD, Kabelik D, Kingsbury MA (2009) Mesotocin and nonapeptide receptors promote estrildid flocking behavior. Science 325:862–866

Grafe TU (2005) Anuran choruses as complex communication networks. In: McGregor PK (ed) Animal communication networks. Cambridge University Press, Cambridge, p 277e299

Grafen A (1998) Evolutionary biology – green beard as death warrant. Nature 394(6693):521–+. doi:10.1038/28948

Grand TC, Dill LM (1999) The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? Anim Behav 58(2):443–451

Grassé PP (1959) La reconstruction du nid et les coordinations inter-individuelles chez Bellicositermes natalensis et Cubitermes sp La theorie de la stigmergie: Essai d'interpretation des termites constructeurs. Insect Soc 6:41–83

Greenwood AK, Wark AR, Yoshida K, Peichel CL (2013) Genetic and neural modularity underlie the evolution of schooling behavior in threespine sticklebacks. Curr Biol 23(19):1884–1888

Gregoire G, Chate H, Tu YH (2003) Moving and staying together without a leader. Phys D Nonlinear Phenom 181(3–4):157–170. doi:10.1016/s0167-2789(03)00102-7

Griffin AS (2004) Social learning about predators: a review and prospectus. Anim Learn Behav 32(1):131–140

Griffin AS (2008) Social learning in Indian mynahs, Acridotheres tristis: the role of distress calls. Anim Behav 75(1):79–89

Griffin RH, Nunn CL (2012) Community structure and the spread of infectious disease in primate social networks. Evolu Ecology 26:779–800

Griffin AS, West SA (2003) Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science 302(5645):634–636

Griffith SC, Owens IP, Thuman KA (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol 11(11):2195–2212

Griffiths SW (2003) Learned recognition of conspecifics by fishes. Fish Fish 4(3):256–268

Griffiths SW, Magurran AE (1997a) Familiarity in schooling fish: how long does it take to acquire? Anim Behav 53:945–949

Griffiths SW, Magurran AE (1997b) Schooling preferences for familiar fish vary with group size in a wild guppy population. Proce Royal Soc London Series B Biol Sci 264(1381): 547–551

Griffiths SW, Brockmark S, Hojesjo J, Johnsson JI (2004) Coping with divided attention: the advantage of familiarity. Proce Royal Soc London Series B Biol Sci 271(1540):695–699. doi:10.1098/rspb.2003.2648

Grinsted L, Bilde T, d'Ettorre P (2011) Cuticular hydrocarbons as potential kin recognition cues in a subsocial spider. Behav Ecology 22(6):1187–1194. doi:10.1093/beheco/arr105

Grosenick L, Clement TS, Fernald RD (2007) Fish can infer social rank by observation alone. Nature 445(7126):429–432. doi:10.1038/nature05511

Grueter CC, van Schaik CP (2010) Evolutionary determinants of modular societies in colobines. Behav Ecology 21:63–71

Grueter CC, Zinner D (2004) Nested societies: convergent adaptations in snub-nosed monkeys and baboons? Primate Rep 70:1–98

Grueter CC, Matsuda I, Zhang P, Zinner D (2012) Multilevel societies in primates and other mammals: introduction to the special issue. Int J Primatol 33:993–1001

Grunbaum D (1998) Schooling as a strategy for taxis in a noisy environment. Evol Ecology 12(5):503–522

Gueron S, Levin SA (1993) Self-organization of front patterns in large wildebeest herds. J Theor Biol 165(4):541–552. doi:10.1006/jtbi.1993.1206

Gueron S, Levin SA, Rubenstein DI (1996) The dynamics of herds: from individuals to aggregations. J Theor Biol 182(1):85–98. doi:10.1006/jtbi.1996.0144

Guhl AM, Collias NE, Allee WC (1945) Mating behavior and the social hierarchy in small flocks of white leghorns. Physiol Zool 18(4):365–390

Guillard J, Fernandes P, Laloe T, Brehmer P (2011) Three-dimensional internal spatial structure of young-of-the-year pelagic freshwater fish provides evidence for the identification of fish school species. Lim Oceanogr Methods 9:322–328. doi:10.4319/lom.2011.9.322

Gumert MD (2007) Payment for sex in a macaque mating market. Anim Behav 74(6):1655–1667

Guttal V, Couzin ID (2010) Social interactions, information use, and the evolution of collective migration. Proc Natl Acad Sci U S A 107:16172–16177

Hager MC, Helfman GS (1991) Safety in numbers – shoal size choice by minnows under predatory threat. Behav Ecology Sociobiology 29:271–276

Halley DJ (2001) Interspecific dominance and risk-taking in three species of corvid scavenger. J Yamashina Institute Ornithol 33:44–50

Halloy J, Sempo G, Caprari G, Rivault C, Asadpour M, Tâche F, Saïd I, Durier V, Canonge S, Amé JM, Detrain C, Correll N, Martinoli A, Mondada F, Siegwart R, Deneubourg JL (2007) Social integration of robots into groups of cockroaches to control self-organized choices. Science 318(5853):1155–1158

Halpin ZT (1980) Individual odors and individual recognition – review and commentary. Biol Behav 5(3):233–248

Hamilton IM (2000) Recruiters and joiners: using optimal skew theory to predict group size and the division of resources within groups of social foragers. Am Nat 155(5):684–695

Hamilton WD (1964) Genetical evolution of social behaviour I. J Theor Biol 7(1):1–16

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31(2):295–311

Hamilton WJ (1967) Social aspects of bird orientation mechanisms. In: Storm RM (ed) Animal orientation and navigation. Oregon State University Press, Corvallis, pp 57–71

Hamner WM, Hamner PP (2000) Behavior of Antarctic krill (Euphausia superba): schooling, foraging, and antipredatory behavior. Can J Fish Aquat Sci 57:192–202

Hamner WM, Hamner PP, Obst BS, Carleton JH (1989) Field observations on the ontogeny of schooling of *Euphausia superba furciliae* and its relationship to ice in antarctic waters. Limnol Oceanogr 34:451–456

Handegard NO, Boswell KM, Ioannou CC, Leblanc SP, Tjostheim DB, Couzin ID (2012) The dynamics of coordinated group hunting and collective information transfer among schooling prey. Curr Biol 22(13):1213–1217. doi:10.1016/j.cub.2012.04.050

Hanlon RT, Messenger JB (1988) Adaptive coloration in young cuttlefish (Sepia officinalis L) – the morphology and development of body patterns and their relation to behavior. Philos T Royal Soc London Series B Biol Sci 320(1200):437. doi:10.1098/rstb.1988.0087

Hansen MJ, Schaerf TM, Ward AJ (2015a) The effect of hunger on the exploratory behaviour of shoals of mosquitofish Gambusia holbrooki. Behav. doi:http://dx.doi.org/10.1163/1568539X-00003298

Hansen MJ, Schaerf TM, Ward AJW (2015b) The influence of nutritional state on individual and group movement behaviour in shoals of crimson-spotted rainbowfish (Melanotaenia duboulayi). Behav Ecolo Soc 69(10):1713–1722. doi:http://dx.doi.org/10.1007/s00265-015-1983-0

Harcourt JL, Ang TZ, Sweetman G, Johnstone RA, Manica A (2009) Social feedback and the emergence of leaders and followers. Curr Biol 19:248–252

Hart BL, Hart LA (1992) Reciprocal allogrooming in impala, *Aepyceros melampus*. Anim Behav 44(6):1073–1083

Hatcher MJ, Tofts C, Franks NR (1992) Mutual exclusion as a mechanism for information exchange within ant nests. Naturwissenschaften 79(1):32–34. doi:10.1007/bf01132279

Hatchwell BJ, Sharp SP, Simeoni M, McGowan A (2009) Factors influencing overnight loss of body mass in the communal roosts of a social bird. Func Ecology 23(2):367–372. doi:10.1111/j.1365-2435.2008.01511.x

Hayes JP, Speakman JR, Racey PA (1992) The contributions of local heating and reducing exposed surface area to the energetic benefits of huddling by short-tailed field voles (Microtus agrestis). Physiol Zool 65:742–762

Hayward JL, Weldon LM, Henson SM, Megna LC, Payne BG, Moncrieff AE (2014) Egg cannibalism in a gull colony increases with sea surface temperature. Condor 116(1):62–73

Heinen JT (1993) Aggregations of newly metamorphosed Bufo americanus: tests of two hypotheses. Can J Zool 71(2):334–338

Heinrich J, Marzluff J (1995) Why Ravens Share. Am Sci 83(4):342–349

Heinsohn RG (1991) Kidnapping and reciprocity in cooperatively breeding white-winged choughs. Anim Behav 41(6):1097–1100

Helbing D, Molnar P (1995) Social force model for pedestrian dynamics. Phy Review E 51(5):4282–4286. doi:10.1103/PhysRevE.51.4282

Helbing D, Vicsek T (1999) Optimal self-organization. New J Phys 1. doi:10.1088/1367-2630/1/1/313

Helbing D, Schweitzer F, Keltsch J, Molnar P (1997) Active walker model for the formation of human and animal trail systems. Phy Rev E 56(3):2527–2539. doi:10.1103/PhysRevE.56.2527

Helfman GS, Schultz ET (1984) Social transmission of behavioral traditions in a coral-reef fish. Anim Behav 32:379–384

Helle T (1980) Abundance of warble fly (*Oedemagena tarandi*) larvae in semi-domestic reindeer (*Rangifer tarandus*) in Finland. Reports Kevo Subarctic Res Station 16:1–6

Helle T, Aspi J, Lempa K, Taskinen E (1992) Strategies to avoid biting flies by reindeer – field experiments with silhouette traps. Ann Zoo Fennici 29(2):69–74

Hemelrijk CK, Hildenbrandt H (2011) Some causes of the variable shape of flocks of birds. Plos One 6(8). doi:10.1371/journal.pone.0022479

Hemelrijk CK, Hildenbrandt H (2012) Schools of fish and flocks of birds: their shape and internal structure by self-organization. Inter Focus 2(6):726–737. doi:10.1098/rsfs.2012.0025

Hemelrijk CK, Kunz H (2005) Density distribution and size sorting in fish schools: an individual-based model. Behav Ecology 16(1):178–187. doi:10.1093/beheco/arh149

Hemelrijk CK, Hildenbrandt H, Reinders J, Stamhuis EJ (2010) Emergence of oblong school shape: models and empirical data of fish. Etholo 116(11):1099–1112. doi:10.1111/j.1439-0310.2010.01818.x

Hendry AP, Peichel CL, Matthews B, Boughman JW, Nosil P (2013) Stickleback research: the now and the next. Evolu Ecology Res 15(2):111–141

Henzi SP, Lusseau D, Weingrill T, van Schaik CP, Barrett L (2009) Cyclicity in the structure of female baboon social networks. Behav Ecol Sociobiol 63(7):1015–1021. doi:10.1007/s00265-009-0720-y

Hepper P (1991) Kin recognition. Cambridge University Press, Cambridge

Herbert-Read JE, Perna A, Mann RP, Schaerf TM, Sumpter DJT, Ward AJW (2011) Inferring the rules of interaction of shoaling fish. Proc Natl Acad Sci U S A 108:18726–18731

Herbert-Read JE, Krause S, Morrell LJ, Schaerf TM, Krause J, Ward AJW (2013) The role of individuality in collective group movement. Proc Royal Soc London B Biol Sci 280(1752):20122564

Herbert-Read JE, Buhl J, Hu F, Ward AJ, Sumpter DJ (2015) Initiation and spread of escape waves within animal groups. Royal Soc Open Sci 2(4):140355

Herczeg G, Gonda A, Merilä J (2009) The social cost of shoaling covaries with predation risk in nine-spined stickleback, Pungitius pungitius, populations. Anim Behav 77(3):575–580

Herskin J, Steffensen JF (1998) Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. J Fish Biol 53(2):366–376

Hesse S, Bakker TCM, Baldauf SA, Thuenken T (2012) Kin recognition by phenotype matching is family- rather than self-referential in juvenile cichlid fish. Anim Behav 84(2):451–457. doi:10.1016/j.anbehav.2012.05.021

Heylighen F (2013) Self-organization in Communicating Groups: the emergence of coordination, shared references and collective intelligence. In: Massip-Bonet A, Bastardas-Boada A (eds) Complexity perspectives on language, communication, and society. Springer, New York, pp 117–149

Higashi M, Yamamura N (1993) What determines animal group size? Insider-outsider conflict and its resolution. Am Natu 142:553–563

Hill SL, Burrows MT, Hughes RN (2003) The efficiency of adaptive search tactics for different prey distribution patterns: a simulation model based on the behaviour of juvenile plaice. J Fish Biol 63(s1):117–130

Hillman JC (1974) Ecology and behavior of the wild eland. Wildlife News 9:6–9

Hillman JC (1979) The biology of the eland (Taurotragus oryx Pallas) in the wild. Nairobi University, Nairobi

Hingee M, Magrath RD (2009) Flights of fear: a mechanical wing whistle sounds the alarm in a flocking bird. Proce Royal Soc London Series B Biol Sci 276:4173–4179

Hirsch BT (2007) Costs and benefits of within-group spatial position: a feeding competition model. Quart Rev Biol 82(1):9–27

Hirsch BT (2011) Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition. Behav Ecolo Soc 65(2):391–399. doi:10.1007/s00265-010-1056-3

Hirsch BT, Morrell LJ (2011) Measuring marginal predation in animal groups. Behav Ecol 22(3):648–656. doi:10.1093/beheco/arr026

Hoare DJ, Krause J (2003) Social organisation, shoal structure and information transfer. Fish Fish 4(3):269–279

Hoare DJ, Krause J, Peuhkuri N, Godin JG (2000a) Body size and shoaling in fish. J Fish Biol 57(6):1351–1366

Hoare DJ, Ruxton GD, Godin JGJ, Krause J (2000b) The social organization of free ranging fish shoals. Oikos 89(3):546–554

Hoare DJ, Couzin ID, Godin JGJ, Krause J (2004) Context-dependent group size choice in fish. Anim Behav 67:155–164. doi:10.1016/j.anbehav.2003.04.004

Hofer H, East ML (2008) Siblicide in Serengeti spotted hyenas: a long-term study of maternal input and cub survival. Behav Ecol Sociobiol 62(3):341–351

Höglund J, Alatalo RV (2014) Leks. Princeton University Press, Princeton

Hogstad O (1987) It is expensive to be dominant. Auk 104(2):333–336

Hogstad O (1988) Social rank and antipredator behavior of willow tits *Parus montanus* in winter flocks. Ibis 130(1):45–56. doi:10.1111/j.1474-919X.1988.tb00954.x

Hogstad O (1989) Subordination in mixed-age bird flocks – a removal study. Ibis 131(1):128–134. doi:10.1111/j.1474-919X.1989.tb02751.x

Hojesjo J, Johnsson JI, Petersson E, Jarvi T (1998) The importance of being familiar: individual recognition and social behavior in sea trout (Salmo trutta). Behav Ecol 9(5):445–451

Holbrook GL, Armstrong E, Bachmann JAS, Deasy BM, Schal C (2000) Role of feeding in the reproductive 'group effect' in females of the German cockroach Blattella germanica (L.). J Insect Physiol 46:941–949

Holekamp KE, Boydston EE, Smale L (2000) Group travel in social carnivores. In: Boinski S, Garber P (eds) On the move: group travel in primates and other animals. University of Chicago Press, Chicago, pp 587–627

Holldobler B, Wilson EO (1970) Recruitment trails in the harvester ant Pogonomyrmex badius. Psyche 77(4):385–399

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, MA, USA

Holldobler B, Wilson EO (2008) The superorganism: the beauty, elegance and strangeness of insect societies. W.W.Norton, New York

Holmes WG (1994) The development of littermate preferences in juvenile beldings ground-squirrels. Anim Behav 48(5):1071–1084. doi:10.1006/anbe.1994.1341

Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in 2 species of ground-squirrels. Am Zool 22(3):491–517

Hoogland JL (1995) The black-tailed prairie dog: social life of a burrowing mammal. The black-tailed prairie dog: social life of a burrowing mammal, University of Chicago Press, Chicago, USA

Hoppitt W, Laland KN (2008) Social processes influencing learning in animals: a review of the evidence. Adv Study Behav 38:105–165

Hoppitt W, Laland KN (2013) Social learning: an introduction to mechanisms, methods, and models. Princeton University Press, Princeton

Houston DC (1974) Food searching in griffon vultures. Afr J Ecol 12(1):63–77

Hrdy SB (1980) The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge

Hughes NF (1992) Ranking of feeding positions by drift-feeding Arctic grayling (Thymallus arcticus) in dominance hierarchies. Can J Fish Aquat Sci 49(10):1994–1998

Hughes WO, Eilenberg J, Boomsma JJ (2002) Trade-offs in group living: transmission and disease resistance in leaf-cutting ants. Proc Royal Soc London B Biol Sci 269(1502):1811–1819

Hughes DP, Kathirithamby J, Turillazzi S, Beani L (2004) Social wasps desert the colony and aggregate outside if parasitized: parasite manipulation? Beha Ecolo 15:1037–1043

Hughes WO, Oldroyd BP, Beekman M, Ratnieks FL (2008) Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science 320(5880):1213–1216

Huizinga M, Ghalambor CK, Reznick DN (2009) The genetic and environmental basis of adaptive differences in shoaling behaviour among populations of Trinidadian guppies, Poecilia reticulata. J Evol Biol 22(9):1860–1866

Hummel D (1995) Formation flight as an energy-saving mechanism. Isr J Zool 41(3):261–278

Hurley AC (1977) School structure of the squid Loligo opalescens. Fishery B NOAA 76:433–442

Hurst JL, Beynon RJ (2004) Scent wars: the chemobiology of competitive signalling in mice. Bioessays 26(12):1288–1298. doi:10.1002/bies.20147

Hutchings MR, Gordon IJ, Kyriazakis I, Jackson F (2001) Sheep avoidance of faeces-contaminated patches leads to a trade-off between intake rate of forage and parasitism in subsequent foraging decisions. Anim Behav 62(5):955–964

Hutchins M, Barash DP (1976) Grooming in primates: implications for its utilitarian function. Primates 17(2):145–150

Huth A, Wissel C (1992) The simulation of the movement of fish schools. J Theor Biol 156(3):365–385. doi:10.1016/s0022-5193(05)80681-2

Ims RA (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. Am Natu 136:485–498

Insley SJ (2000) Long-term vocal recognition in the northern fur seal. Nature 406(6794):404–405. doi:10.1038/35019064

Insley SJ, Phillips AV, Charrier I (2003) A review of social recognition in pinnipeds. Aqu Mamm 29(2):181–201. doi:10.1578/016754203101024149

Ioannou CC, Tosh CR, Neville L, Krause J (2008) The confusion effect—from neural networks to reduced predation risk. Behav Ecolo 19(1):126–130

Ioannou CC, Morrell LJ, Ruxton GD, Krause J (2009) The effect of prey density on predators: conspicuousness and attack success are sensitive to spatial scale. Am Nat 173(4):499–506

Ioannou CC, Bartumeus F, Krause J, Ruxton GD (2011) Unified effects of aggregation reveal larger prey groups take longer to find. Proce Royal Soc B Biol Sci 278(1720):2985–2990

Ioannou CC, Guttal V, Couzin ID (2012) Predatory fish select for coordinated collective motion in virtual prey. Science 337(6099):1212–1215

Ioannou CC, Singh M, Couzin ID (2015) Potential leaders trade off goal-oriented and socially oriented behavior in mobile animal groups. American Naturalist 186(2):284–293

Issa FA, Edwards DH (2006) Ritualized submission and the reduction of aggression in an invertebrate. Curr Biol 16(22):2217–2221. doi:10.1016/j.cub.2006.08.065

Jackson DE, Ratnieks FL (2006) Communication in ants. Curr Biol 16(15):R570–R574

Jackson AL, Ruxton GD, Houston DC (2008) The effect of social facilitation on foraging success in vultures: a modelling study. Biol Lett 4(3):311–313

Jaeger RG (1981) Dear enemy recognition and the costs of aggression between salamanders. Am Natu 117(6):962–974

Jakobsen PJ, Johnsen GH (1988) Size-specific protection against predation by fish in swarming waterfleas, Bosmina longispina. Anim Behav 36:986–990. doi:10.1016/s0003-3472(88)80057-5

Jakobsson S, Brick O, Kullberg C (1995) Escalated fighting behaviour incurs increased predation risk. Anim Behav 49(1):235–239

James R, Bennett PG, Krause J (2004) Geometry for mutualistic and selfish herds: the limited domain of danger. J Theor Biol 228(1):107–113. doi:10.1016/j.jtbi.2003.12.005

Jander R, Daumer K (1974) Guide-line and gravity orientation of blind termites foraging in open (Termitidae macrotermes, Hospitalitermes). Insectes Socia 21(1):45–69. doi:10.1007/bf02222979

Janik VM, Sayigh LS, Wells RS (2006) Signature whistle shape conveys identity information to bottlenose dolphins. Proc Natl Acad Sci U S A 103(21):8293–8297. doi:10.1073/pnas.0509918103

Jarman P (1974) The social organisation of antelope in relation to their ecology. Behaviour 48(1):215–267

Jeanson R, Rivault C, Deneubourg JL, Blanco S, Fournier R, Jost C, Theraulaz G (2005) Self-organized aggregation in cockroaches. Anim Behav 69:169–180. doi:10.1016/j.anbehav.204.02.009

Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72(2):283–327

Jiguet F, Bretagnolle V (2006) Manipulating lek size and composition using decoys: an experimental investigation of lek evolution models. Am Nat 168(6):758–768

Johannesen J, Lubin Y (2001) Evidence for kin-structured group founding and limited juvenile dispersal in the sub-social spider Stegodyphus lineatus (Araneae, Eresidae). J Arachnol 29(3):413–422. doi:10.1636/0161-8202(2001)029[0413:efksgf]2.0.co;2

Johansen JL, Vaknin R, Steffensen JF, Domenici P (2010) Kinematics and energetic benefits of schooling in the labriform fish, striped surfperch Embiotoca lateralis. Mar Ecol Prog Ser 420:221–229. doi:10.3354/meps08885

Johnsen TS, Hengeveld JD, Blank JL, Yasukawa K, Nolan V (1996) Epaulet brightness and condition in female red-winged blackbirds. Auk 113(2):356–362

Johnson PT, Dobson A, Lafferty KD, Marcogliese DJ, Memmott J, Orlofske SA, Poulin R, Thieltges DW (2010) When parasites become prey: ecological and epidemiological significance of eating parasites. Trends Ecol Evol 25(6):362–371

Johnston RE (2003) Chemical communication in rodents: from pheromones to individual recognition. J Mammal 84(4):1141–1162. doi:10.1644/BLe-010

Jolles JW, King AJ, Manica A, Thornton A (2013) Heterogeneous structure in mixed-species corvid flocks in flight. Anim Behav 85(4):743–750

Jolles JW, Fleetwood-Wilson A, Nakayama S, Stumpe MC, Johnstone RA, Manica A (2014) The role of previous social experience on risk-taking and leadership in three-spined sticklebacks. Behavioral Ecology, aru146

Jolles JW, Fleetwood-Wilson A, Nakayama S, Stumpe MC, Johnstone RA, Manica A (2015) The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. Anim Behav 99:147–153

Jolly A (1985) The evolution of primate behavior. Am Sci 73:230–239

Jones TM, Quinnell RJ (2002) Testing predictions for the evolution of lekking in the sandfly, Lutzomyia longipalpis. Anim Behav 63(3):605–612

Jordan LA, Avolio C, Herbert-Read JE, Krause J, Rubenstein DI, Ward AJW (2010) Group structure in a restricted entry system is mediated by both resident and joiner preferences. Behav Ecol Sociobiol 64:1099–1106

Jouventin P, Aubin T, Lengagne T (1999) Finding a parent in a king penguin colony: the acoustic system of individual recognition. Anim Behav 57:1175–1183. doi:10.1006/anbe.1999.1086

Judd TM, Sherman PW (1996) Naked mole-rats recruit colony mates to food sources. Anim Behav 52:957–969

Kao AB, Couzin ID (2014) Decision accuracy in complex environments is often maximized by small group sizes. Proc Royal Soc B Biol Sci 281:20133305

Karavanich C, Atema J (1998) Individual recognition and memory in lobster dominance. Anim Behav 56:1553–1560. doi:10.1006/anbe.1998.0914

Karvonen A, Seppala O, Valtonen ET (2004) Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. Parasitology 129:159–164

Katz Y, Tunstrom K, Ioannou CC, Huepe C, Couzin ID (2011) Inferring the structure and dynamics of interactions in schooling fish. Proc Natl Acad Sci U S A 108(46):18720–18725. doi:10.1073/pnas.1107583108

Kavaliers M, Choleris E, Agmo A, Pfaff DW (2004) Olfactory-mediated parasite recognition and avoidance: linking genes to behavior. Horm Behav 46:272–283

Kavaliers M, Choleris E, Pfaff DW (2005) Genes, odours and the recognition of parasitized individuals by rodents. Trends Parasitol 21:423–429

Keenleyside MHA (1955) Some aspects of the schooling behaviour of fish. Behaviour 8:83–248

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends Ecol Evol 9(3):98–102

Keller L, Ross KG (1998) Selfish genes: a green beard in the red fire ant. Nature 394(6693):573–575. doi:10.1038/29064

Kelley DH, Ouellette NT (2013) Emergent dynamics of laboratory insect swarms. Sci R 3. doi:10.1038/srep01073

Kendrick KM, da Costa AP, Leigh AE, Hinton MR, Peirce JW (2001) Sheep don't forget a face. Nature 414(6860):165–166. doi:10.1038/35102669

Kershenbaum A, Sayigh LS, Janik VM (2013) The encoding of individual identity in Dolphin signature whistles: how much information is needed?. Plos One 8 (10). doi:10.1371/journal.pone.0077671

Kerth G, Ebert C, Schmidtke C (2006) Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. Proc Royal Soc B Biol Sci 273:2785–2790. doi:10.1098/rspb.2006.3647

Keverne EB, Martensz ND, Tuite B (1989) Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. Psychoneuroendocrinology 14(1):155–161

Keys GC, Dugatkin LA (1990) Flock size and position effects on vigilance, aggression, and prey capture in the European starling. Condor 92(1):151–159. doi:10.2307/1368393

King AJ (2010) Follow me! I'm a leader if you do; I'm a failed initiator if you don't? Behav Processes 84:671–674

King AJ, Cowlishaw G (2009) All together now: behavioural synchrony in baboons. Anim Behav 78(6):1381–1387. doi:10.1016/j.anbehav.2009.09.009

King KA, Keith JO, Mitchell CA, Keirans JA (1977a) Ticks as a factor in nest desertion of California Brown Pelicans. Condor 79:507–509

King KA, Blankinship DR, Paul RT, Rice RCA (1977b) Ticks as a factor in the 1975 nesting failure of Texas Brown Pelicans. Wilson B 89:157–158

King AJ, Isaac NJB, Cowlishaw G (2009) Ecological, social and reproductive factors shape producer-scrounger dynamics in wild baboons. Behav Ecolo 20:1039–1049

King AJ, Wilson AM, Wilshin SD, Lowe J, Haddadi H, Hailes S, Morton AJ (2012) Selfish-herd behaviour of sheep under threat. Curr Biol 22:R561–R562

King AJ, Williams LJ, Mettke-Hofmann C (2015) The effects of social conformity on Gouldian finch personality. Anim Behav 99:25–31. doi:10.1016/j.anbehav.2014.10.016

Kingdon J (1982) Bovids. East African mammals: an atlas of evolution in Africa. University of Chicago Press, Chicago, USA

Kleiman DG (2011) Canid mating systems, social behavior, parental care and ontogeny: are they flexible? Behav Genet 41:803–809

Klok CJ, Chown SL (1999) Assessing the benefits of aggregation: thermal biology and water relations of anomalous Emperor Moth caterpillars. Fun Ecolo 13(3):417–427

Koivula K, Lahti K, Rytkonen S, Orell M (1994) Do subordinates expose themselves to predation – field experiments on feeding site selection by willow TITS. J Avian Biol 25(3):178–183. doi:10.2307/3677073

Kokko H, Johnstone RA (1999) Social queuing in animal societies: a dynamic model of reproductive skew. Proc Royal Soc B Biol Sci 266(1419):571–578

Kokko H, Johnstone RA, Clutton-Brock TH (2001) The evolution of cooperative breeding through group augmentation. Proc Royal Soc B Biol Sci 268(1463):187–196

Kolmes SA (1989) Grooming specialists among worker honey bees, Apis mellifera. Anim Behav 37:1048–1049

Komdeur J, Hatchwell BJ (1999) Kin recognition: function and mechanism in avian societies. Trends Ecol Evol 14(6):237–241. doi:10.1016/s0169-5347(98)01573-0

Kozak GM, Boughman JW (2008) Experience influences shoal member preference in a species pair of sticklebacks. Behav Ecolo 19:667–676

Krakauer DC (1995) Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. Behav Ecol Sociobiol 36(6):421–429

Kramer DL, Manley D, Bourgeois R (1983) The effect of respiratory mode and oxygen concentration on the risk of aerial predation in fishes. Can J Zool 61(3):653–665

Krams I (1998) Rank-dependent fattening strategies of Willow Tit Parus montanus and Crested Tit P-cristatus mixed flock members. Ornis Fennica 75(1):19–26

Krams I, Krama T, Igaune K, Mänd R (2008) Experimental evidence of reciprocal altruism in the pied flycatcher. Behav Ecol Sociobiol 62(4):599–605. doi:10.1007/s00265-007-0484-1

Krause J (1993a) The effect of schreckstoff on the shoaling behavior of the minnow – a test of Hamilton's selfish herd theory. Anim Behav 45(5):1019–1024. doi:10.1006/anbe.1993.1119

Krause J (1993b) The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*) – a field-study. Oecologia 93(3):356–359

Krause J (1994) Differential fitness returns in relation to spatial position in groups. Biol Rev Camb Philos Soc 69(2):187–206

Krause J, Godin JGJ (1994) Influence of parasitism on the shoaling behavior of banded killifish, Fundulus diaphanus. Can J Zool Revue Can De Zool 72:1775–1779

Krause J, Godin JGJ (1996a) Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. Behav Ecolo 7(3):264–271

Krause J, Godin JGJ (1996b) Influence of parasitism on shoal choice in the banded killifish (Fundulus diaphanus, Teleostei, Cyprinodontidae). Ethology 102:40–49

Krause J, Ruxton GD (2002) Living in groups. OUP, Oxford

Krause J, Bumann D, Todt D (1992) Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (Rutilus rutilus). Behav Ecolo Soc 30(3–4):177–180

Krause J, Reeves P, Hoare D (1998a) Positioning behaviour in roach shoals: the role of body length and nutritional state. Behaviour 135:1031–1039

Krause J, Ruxton GD, Rubenstein D (1998b) Is there always an influence of shoal size on predator hunting success? J Fish Biol 52(3):494–501

Krause J, Hartmann N, Pritchard VL (1999) The influence of nutritional state on shoal choice in zebrafish, Danio rerio. Anim Behav 57(4):771–775

Krause J, Hoare DJ, Krause S, Hemelrijk CK, Rubenstein DI (2000) Leadership in fish shoals. Fish Fish 1:82–89

Krause J, Ward AJW, Jackson AL, Ruxton GD, James R, Currie S (2005) The influence of differential swimming speeds on composition of multi-species fish shoals. J Fish Biol 67(3):866–872. doi:10.1111/j.1095-8649.2005.00769.x

Krause J, Ruxton GD, Krause S (2010) Swarm intelligence in animals and humans. Trends Ecol Evol 25:28–34

Krebs JR (1974) Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51(1):99–134

Kruijt JP (1964) Ontogeny of social behaviour in Burmese red junglefowl (*Gallus gallus spadiceus*). Behav Suppl 12:1–201

Kruuk H (1964) Predators and antipredator behaviour of the black-headed gull (*Larus ridibundus*). Behav Suppl 11:1–129

Kulahci IG, Drea CM, Rubenstein DI, Ghazanfar AA (2014) Individual recognition through olfactory – auditory matching in lemurs. Proc Royal Soc B Biolo Sci 281(1784). doi:10.1098/rspb.2014.0071

Kummer H (1971) Primate societies: group techniques of ecological adaptation. Aldine-Atherton, Chicago

Kuramoto Y (1984) Chemical oscillations, waves, and turbulence. Springer, Berlin

Kurvers R, Eijkelenkamp B, van Oers K, van Lith B, van Wieren SE, Ydenberg RC, Prins HHT (2009) Personality differences explain leadership in barnacle geese. Anim Behav 78:447–453

Kurvers R, Adamczyk V, Kraus RHS, Hoffman JI, van Wieren SE, van der Jeugd HP, Amos W, Prins HHT, Jonker RM (2013) Contrasting context dependence of familiarity and kinship in animal social networks. Anim Behav 86(5):993–1001. doi:10.1016/j.anbehav.2013.09.001

Lafferty KD, Shaw JC (2013) Comparing mechanisms of host manipulation across host and parasite taxa. J Exp Biol 216:56–66

Lahti K (1998) Social dominance and survival in flocking passerine birds: a review with an emphasis on the Willow Tit Parus montanus. Ornis Fennica 75(1):1–17

Lahti K, Koivula K, Orell M (1997) Dominance, daily activity and winter survival in willow tits: detrimental cost of long working hours? Behaviour 134:921–939. doi:10.1163/156853997x00232

Laidre ME (2013) Eavesdropping foragers use level of collective commotion as public information to target high quality patches. Oikos 122(10):1505–1511

Lack DL (1968). Ecological adaptations for breeding in birds.

Laland KN (2004) Social learning strategies. Anim Learn Behav 32(1):4–14

Laland KN, Galef BG (2009) The question of animal culture. Harvard University Press, Cambridge/London

Laland KN, Hoppitt W (2003) Do animals have culture? Evol Anth Iss News Rev 12(3):150–159

Laland KN, Janik VM (2006) The animal cultures debate. Trends Ecol Evol 21(10):542–547

Laland KN, Williams K (1997) Shoaling generates social learning of foraging information in guppies. Anim Behav 53(6):1161–1169

Laland KN, Williams K (1998) Social transmission of maladaptive information in the guppy. Behav Ecolo 9:493–499

Laland KN, Odling-Smee J, Myles S (2010) How culture shaped the human genome: bringing genetics and the human sciences together. Nat Rev Genet 11(2):137–148

Laland KN, Atton N, Webster MM (2011) From fish to fashion: experimental and theoretical insights into the evolution of culture. Phil Tran Royal Soc B Biol Sci 366(1567):958–968

Lancaster J (1971) Play-mothering – relations between juvenile females and young infants among free-ranging vervet monkeys – *Cercopithecus aethiops*. Folia Primatol 15(3–4):161. doi:10.1159/000155377

Landeau L, Terborgh J (1986) Oddity and the 'confusion effect' in predation. Anim Behav 34(5):1372–1380

Langen TA, Rabenold KN (1994) Dominance and diet selection in juncos. Behav Ecolo 5(3):334–338. doi:10.1093/beheco/5.3.334

Launay F, Mills AD, Faure JM (1991) Social motivation in japanese-quail coturnix-coturnix-japonica chicks selected for high or low-levels of treadmill behavior. Behav Processes 24(2):95–110. doi:10.1016/0376-6357(91)90002-h

Lazarus J (1979) Flock size and behaviour in captive red-billed weaverbirds (Quelea quelea): implications for social facilitation and the functions of flocking. Behaviour 71(1):127–144

Leadbeater E, Dapporto L, Turillazzi S, Field J (2014) Available kin recognition cues may explain why wasp behavior reflects relatedness to nest mates. Behav Ecolo 25(2):344–351. doi:10.1093/beheco/art113

Leca JB, Gunst N, Thierry B, Petit O (2003) Distributed leadership in semifree-ranging white-faced capuchin monkeys. Anim Behav 66:1045–1052

Lecchini D, Nakamura Y (2013) Use of chemical cues by coral reef animal larvae for habitat selection. Aquat Biol 19(3):231–238. doi:10.3354/ab00532

Lee-Jenkins SS, Smith ML, Wisenden BD, Wong A, Godin JGJ (2015) Genetic evidence for mixed broods and extra-pair matings in a socially monogamous biparental cichlid fish. Behaviour. doi:10.1163/1568539X-00003289

Lefebvre L, Palameta B, Hatch KK (1996) Is group-living associated with social learning? A comparative test of a gregarious and a territorial columbid. Behaviour 133(3):241–261

Lemasson BH, Anderson JJ, Goodwin RA (2009) Collective motion in animal groups from a neurobiological perspective: the adaptive benefits of dynamic sensory loads and selective attention. J Theor Biol 261(4):501–510. doi:10.1016/j.jtbi.2009.08.013

Leonard NE, Shen T, Nabet B, Scardovi L, Couzin ID, Levin SA (2012) Decision versus compromise for animal groups in motion. Proc Natl Acad Sci U S A 109:227–232

Leopold DA, Rhodes G (2010) A comparative view of face perception. J Comp Psychol 124(3):233–251. doi:10.1037/a0019460

Leopold DA, Rhodes G, Muller KM, Jeffery L (2005) The dynamics of visual adaptation to faces. Proc Royal Soc B Biol Sci 272(1566):897–904. doi:10.1098/rspb.2004.3022

Levin S (1997) Conceptual and methodological issues in the modeling of biological aggregations. In: Parrish JK, Hamner WM (eds) Animal groups in three dimensions. Cambridge University Press, Cambridge, pp 247–256

Lewis SE, Hodel A, Sturdy T, Todd R, Weigl C (2012) Impact of acanthocephalan parasites on aggregation behavior of amphipods (Gammarus pseudolimnaeus). Behav Processes 91:159–163

Liao X, Rong S, Queller DC (2015) Relatedness, conflict, and the evolution of eusociality. PLoS Biol 13(3):e1002098

Lickliter RE (1987) Activity patterns and companion preferences of domestic goat kids. Appl Anim Behav Sci 19:137–145

Liebert AE, Starks PT (2004) The action component of recognition systems: a focus on the response. Ann Zool Fennici 41(6):747–764

Lihoreau M, Rivault C (2008) Tactile stimuli trigger group effects in cockroach aggregations. Anim Behav 75:1965–1972

Lihoreau M, Rivault C (2009) Kin recognition via cuticular hydrocarbons shapes cockroach social life. Behav Ecolo 20(1):46–53. doi:10.1093/beheco/arn113

Liker A, Bokony V (2009) Larger groups are more successful in innovative problem solving in house sparrows. Proc Natl Acad Sci U S A 106:7893–7898

Lill A (1974) Sexual Behavior of the Lek-forming White-bearded Manakin (Manacus manacus trinitatis Hartert). Z Tierpsychol 36(1–5):1–36

Lima SL (1995) Collective detection of predatory attack by social foragers – fraught with ambiguity. Anim Behav 50:1097–1108

Lindström L (1999) Experimental approaches to studying the initial evolution of conspicuous aposematic signalling. Evolu Ecolo 13(7–8):605–618

Lingle S, Wyman MT, Kotrba R, Teichroeb LJ, Romanow CA (2012) What makes a cry a cry? A review of infant distress vocalizations. Curr Zool 58(5):698–726

Lipkind D, Nottebohm F, Rado R, Barnea A (2002) Social change affects the survival of new neurons in the forebrain of adult songbirds. Behav Brain Res 133:31–43

Lissaman PB, Shollenberger CA (1970) Formation flight of birds. Science 168(3934):1003. doi:10.1126/science.168.3934.1003

List C (2004) Democracy in animal groups: a political science perspective. Trends Ecol Evol 19:168–169

Lloyd PH, Rasa OAE (1989) Status, reproductive success and fitness in cape mountain zebra (equus-zebra-zebra). Behav Ecol Sociobiol 25(6):411–420. doi:10.1007/bf00300187

Lorch JM, Meteyer CU, Behr MJ, Boyles JG, Cryan PM, Hicks AC, Ballmann AE, Coleman JT, Redell DN, Reeder DM, Blehert DS (2011) Experimental infection of bats with Geomyces destructans causes white-nose syndrome. Nature 480(7377):376–378

Lubbock R (1980) Why are clownfishes not stung by sea-anemones. Proc R Soc Ser B Biol Sci 207(1166):35. doi:10.1098/rspb.1980.0013

Lubin Y, Henschel JR, Baker MB (2001) Costs of aggregation: shadow competition in a sit-and-wait predator. Oikos 95(1):59–68

Lukeman R, Li YX, Edelstein-Keshet L (2010) Inferring individual rules from collective behavior. Proc Natl Acad Sci U S A 107(28):12576–12580. doi:10.1073/pnas.1001763107

Lukkes JL, Mokin MV, Scholl JL, Forster GL (2009) Adult rats exposed to early-life social isolation exhibit increased anxiety and conditioned fear behavior, and altered hormonal stress responses. Horm Behav 55:248–256

Lupfer-Johnson G, Ross J (2007) Dogs acquire food preferences from interacting with recently fed conspecifics. Behav Processes 74(1):104–106

Lupfer-Johnson G, Hanson KL, Edwards LE, Elder RL, Evans SL (2009) Social cues influence foraging in dwarf hamsters (Phodopus campbelli). J Comp Psychol 123(2):226–229

Lurling M, Scheffer M (2007) Info-disruption: pollution and the transfer of chemical information between organisms. Trends Ecol Evol 22:374–379

Lusseau D (2003) The emergent properties of a dolphin social network. Proc Roy Soc London Ser B Biol Sci 270:S186–S188

Mackenzie A, Reynolds JD, Brown VJ, Sutherland WJ (1995) Variation in male mating success on leks. Am Nat 145:633–652

Maeno K, Tanaka S (2010) Epigenetic transmission of phase in the desert locust, Schistocerca gregaria determining the stage sensitive to crowding for the maternal determination of progeny characteristics. J Insect Physiol 56:1883–1888

Maestripieri D (1993) Vigilance costs of allogrooming in macaque mothers. Am Nat 141: 744–753

Magurran AE (1998) Population differentiation without speciation. Phil Tran Royal Soc B Biol Sci 353(1366):275–286

Magurran AE (2005) Evolutionary ecology: the Trinidadian guppy. Oxford University Press, Oxford

Magurran AE, Higham A (1988) Information transfer across fish shoals under predator threat. Etholo 78(2):153–158

Magurran AE, Seghers BH (1994) A cost of sexual harassment in the guppy, Poecilia reticulata. Proc Royal Soc London Series B Biol Sci 258(1351):89–92

Magurran AE, Seghers BH, Carvalho GR, Shaw PW (1992) Behavioural consequences of an artificial introduction of guppies (Poecilia reticulata) in N. Trinidad: evidence for the evolution of anti-predator behaviour in the wild. Proc Royal Soc London Series B Biol Sci 248(1322):117–122

Magurran AE, Seghers BH, Shaw PW, Carvalho GR (1995) The behavioral diversity and evolution of guppy, Poecilia reticulata, populations in Trinidad. Adv Study Behav 24:155–202

Mahurin EJ, Freeberg TM (2009) Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. Behav Ecolo 20(1):111–116

Major PF (1977) Predator–prey interactions in schooling fishes during periods of twilight: a study of the silverside Pranesus insulanrm in Hawaii. Fishery B NOAA 75:415–426

Major PF, Dill LM (1978) 3-dimensional structure of airborne bird flocks. Behav Ecol Sociobiol 4(2):111–122. doi:10.1007/bf00354974

Makris NC, Ratilal P, Jagannathan S, Gong Z, Andrews M, Bertsatos I, Godo OR, Nero RW, Jech JM (2009) Critical population density triggers rapid formation of vast oceanic fish shoals. Science 323(5922):1734–1737. doi:10.1126/science.1169441

Mann RP, Perna A, Strombom D, Garnett R, Herbert-Read JE, Sumpter DJT, Ward AJW (2013) Multi-scale inference of interaction rules in animal groups using Bayesian Model Selection. Plos Compu Biolo 9(3). doi:10.1371/journal.pcbi.1002961

Mappes J, Marples N, Endler JA (2005) The complex business of survival by aposematism. Trends Ecol Evol 20(11):598–603

Masuda R, Tsukamoto K (1999) School formation and concurrent developmental changes in carangid fish with reference to dietary conditions. Environ Biol Fishes 56:243–252

Mateo JM (2004) Recognition systems and biological organization: the perception component of social recognition. Ann Zool Fennici 41(6):729–745

Mateo JM (2006) The nature and representation of individual recognition odours in Belding's ground squirrels. Anim Behav 71:141–154. doi:10.1016/j.anbehav.2005.04.006

Mateo JM (2009) The causal role of odours in the development of recognition templates and social preferences. Anim Behav 77(1):115–121. doi:10.1016/j.anbehav.2008.09.015

Mateo JM (2010) Self-referent phenotype matching and long-term maintenance of kin recognition. Anim Behav 80(5):929–935. doi:10.1016/j.anbehav.2010.08.019

Mathis A, Chivers DP, Smith RJF (1995) Chemical alarm signals: predator deterrents or predator attractants? Am Nat 145:994–1005

Mathis A, Ferrari MC, Windel N, Messier F, Chivers DP (2008) Learning by embryos and the ghost of predation future. Proc Royal Soc London B Biol Sci 275(1651):2603–2607

Mathot KJ, Dingemanse NJ (2015a) Energetics and behavior: unrequited needs and new directions. Trends Ecol Evol 30:199–206

Mathot KJ, Dingemanse NJ (2015b) Energetics and behaviour: a reply to Careau and Garland. Trends Ecol Evol 30:367–368

Matsumura K, Matsunaga S, Fusetani N (2004) Possible involvement of phosphatidylcholine in school recognition in the catfish, *Plotosus lineatus*. Zoolog Sci 21(3):257–264

Matthews IM, Magurran AE (2000) Evidence for sperm transfer during sneaky mating in wild Trinidadian guppies. J Fish Biol 56(6):1381–1386

Maynard Smith J (1964) Group selection and kin selection. Nature 201:1145–1147

McCaffery AR, Simpson SJ, Islam MS, Roessingh P (1998) A gregarizing factor present in the egg pod foam of the desert locust Schistocerca gregaria. J Exper Biol 201:347–363

McCarthy ID, Carter CG, Houlihan DF (1992) The effect of feeding hierarchy on individual variability in daily feeding of rainbow trout, Oncorhynchus mykiss (Walbaum). J Fish Biol 41(2):257–263

McComb K, Moss C, Sayialel S, Baker L (2000) Unusually extensive networks of vocal recognition in African elephants. Anim Behav 59:1103–1109. doi:10.1006/anbe.2000.1406

McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories of social knowledge in African elephants. Science 292:491–494

McComb K, Reby D, Baker L, Moss C, Sayialel S (2003) Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav 65:317–329. doi:10.1006/anbe.2003.2047

McFarland W, Okubo A (1997) Metabolic models of fish school behavior – the need for quantitative observations. In: Parrish JK, Hamner WM (eds) Animal groups in three dimensions. Cambridge University Press, Cambridge, pp 301–312

McGregor PK (2005) Animal communication networks. Cambridge University Press, New York

Mebs D (2009) Chemical biology of the mutualistic relationships of sea anemones with fish and crustaceans. Toxicon 54(8):1071–1074. doi:10.1016/j.toxicon.2009.02.027

Mech LD (1970) The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City

Mennill DJ, Doucet SM, Montgomerie R, Ratcliffe LM (2003) Achromatic color variation in black-capped chickadees, Poecile atricapilla: black and white signals of sex and rank. Behav Ecol Sociobiol 53(6):350–357. doi:10.1007/s00265-003-0581-8

Metcalfe NB, Thomson BC (1995) Fish recognize and prefer to shoal with poor competitors. Proc Roy Soc London Ser B Biol Sci 259(1355):207–210

Michelena P, Henric K, Angibault JM, Gautrais J, Lapeyronie P, Porter RH, Deneubourg JL, Bon R (2005) An experimental study of social attraction and spacing between the sexes in sheep. J Exp Biol 208(23):4419–4426. doi:10.1242/jeb.01909

Michelena P, Gautrais J, Gerard JF, Bon R, Deneubourg JL (2008) Social cohesion in groups of sheep: effect of activity level, sex composition and group size. Appl Anim Behav Sci 112(1–2):81–93. doi:10.1016/j.applanim.2007.06.020

Michelena P, Sibbald AM, Erhard HW, McLeod JE (2009) Effects of group size and personality on social foraging: the distribution of sheep across patches. Behav Ecolo 20:145–152

Miklosi A, Topal J, Csanyi V (2004) Comparative social cognition: what can dogs teach us? Anim Behav 67:995–1004. doi:10.1016/j.anbehav.2003.10.008

Milinski M (1987) Tit for tat in sticklebacks and the evolution of cooperation. Nature 325(6103):433–435

Milinski M, David K, Kettler R (1990) Tit for tat: sticklebacks (*Gasterosteus aculeatus*) 'trusting'a cooperating partner. Behav Ecolo 1(1):7–11

Miller N, Garnier S, Hartnett AT, Couzin ID (2013) Both information and social cohesion determine collective decisions in animal groups. Proc Natl Acad Sci U S A 110:5263–5268

Mills AD, Faure JM (1990) The treadmill test for the measurement of social motivation in phasianidae chicks. Med Sci Res 18(5):179–180

Milner RN, Jennions MD, Backwell PR (2010) Eavesdropping in crabs: an agency for lady detection. Biol Lett 6:755e757

Mineka S, Cook M (1988) Social learning and the acquisition of snake fear in monkeys. In Zentall TR, Galef Jr. BG (Eds) Social learning: Psychological and biological perspectives, p. 51–73. Hillsdale, New Jersey USA

Mock DW, Parker GA (1998) Siblicide, family conflict and the evolutionary limits of selfishness. Anim Behav 56(1):1–10

Mock DW, Lamey TC, Ploger BJ (1987) Proximate and ultimate roles of food amount in regulating egret sibling aggression. Ecology 68:1760–1772

Mock DW, Drummond H, Stinson CH (1990) Avian siblicide. Am Sci 78:438–449

Möglich M, Hölldobler B (1974) Social carrying behavior and division of labor during nest moving in ants. Psyche 81:219–236

Møller AP, Allander K, Dufva R (1990) Fitness effects of parasites on passerine birds: a review. In: Population biology of passerine birds. Springer, Berlin/Heidelberg, pp 269–280

Møller AP, Dufva R, Allander K (1993) Parasites and the evolution of host social behavior. Adv Study Behav 22(65):102

Moore A, Ives MJ, Kell LT (1994) The role of urine in sibling recognition in Atlantic salmon *Salmo salar* parr. Proc Roy Soc London Ser B Biol Sci 255(1343):173–180

Moore D, Angel JE, Cheeseman IM, Robinson GE, Fahrbach SE (1995) A highly specialized social grooming honey bee (Hymenoptera: Apidae). J Ins Behavior 8(6):855–861

Moore H, Dvorakova K, Jenkins N, Breed W (2002) Exceptional sperm cooperation in the wood mouse. Nature 418(6894):174–177. doi:10.1038/nature00832

Mooring MS, Hart BL (1992) Animal grouping for protection from parasites – selfish herd and encounter-dilution effects. Behaviour 123:173–193

Mooring MS, Hart BL (1995) Costs of allogrooming in impala: distraction from vigilance. Anim Behav 49(5):1414–1416

Moreno J, Bustamante J, Viñuela J (1995) Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis antarctica*). Polar Biol 15(8):533–540

Morrell LJ, Ruxton GD, James R (2011) Spatial positioning in the selfish herd. Behav Ecolo 22(1):16–22. doi:10.1093/beheco/arq157

Morse DH (1970) Ecological aspects of some mixed-species foraging flocks of birds. Ecolo Monogra 40:119–168

Morse DH (1978) Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. Ibis 120(3):298–312

Mottley K, Giraldeau LA (2000) Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. Anim Behav 60(3):341–350

Mougenot F, Combe M, Jeanson R (2012) Ontogenesis and dynamics of aggregation in a solitary spider. Anim Behav 84:391–398

Moussaid M, Garnier S, Theraulaz G, Helbing D (2009) Collective information processing and pattern formation in swarms, flocks, and crowds. Topics Cognitive Sci 1:469–497

Mueller T, O'Hara RB, Converse SJ, Urbanek RP, Fagan WF (2013) Social learning of migratory performance. Science 341(6149):999–1002

Mulder RA, Dunn PO, Cockburn A, Lazenby-Cohen KA, Howell MJ (1994) Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. Proc Royal Soc London B Biol Sci 255(1344):223–229

Muleta MG, Schausberger P (2013) Smells familiar: group-joining decisions of predatory mites are mediated by olfactory cues of social familiarity. Anim Behav 86(3):507–512. doi:10.1016/j.anbehav.2013.05.040

Müller CA, Bell MB (2009) Kidnapping and infanticide between groups of banded mongooses. Mammalian Biol Zeitschrift für Säugetierkunde 74(4):315–318

Nagy M, Akos Z, Biro D, Vicsek T (2010) Hierarchical group dynamics in pigeon flocks. Nature 464:890

Nagy M, Vasarhelyi G, Pettit B, Roberts-Mariani I, Vicsek T, Biro D (2013) Context-dependent hierarchies in pigeons. Proc Natl Acad Sci U S A 110:13049–13054

Nakamura T, Croft DB, Westbrook RF (2003) Domestic pigeons (Columba livia) discriminate between photographs of individual pigeons. Learn Behav 31(4):307–317

Nakayama S, Harcourt JL, Johnstone RA, Manica A (2012) Initiative, personality and leadership in pairs of foraging fish. PLoS One 7(5):e36606

Napper CJ, Sharp SP, McGowan A, Simeoni M, Hatchwell BJ (2013) Dominance, not kinship, determines individual position within the communal roosts of a cooperatively breeding bird. Behav Ecol Sociobiol 67(12):2029–2039. doi:10.1007/s00265-013-1613-7

Neda Z, Ravasz E, Brechet Y, Vicsek T, Barabasi AL (2000) The sound of many hands clapping – tumultuous applause can transform itself into waves of synchronized clapping. Nature 403(6772):849–850. doi:10.1038/35002660

Neill S, Cullen JM (1974) Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J Zool 172(4):549–569

Nelson RJ (2000) An introduction to behavioral endocrinology. Sinauer Associates, Sunderland

Neuswanger J, Wipfli MS, Rosenberger AE, Hughes NF (2014) Mechanisms of drift-feeding behavior in juvenile Chinook salmon and the role of inedible debris in a clear-water Alaskan stream. Environ Biol Fishes 97(5):489–503

Newson RM, Mella PNP, Franklin TE (1973) Observations on the numbers of the tick *Rhipicephalus appendiculatus* on the ears of zebu cattle in relation to hierarchical status in the herd. Tropl Anim Health Prod 5(4):281–283. doi:10.1007/bf02240430

Nicieza AG (1999) Context-dependent aggregation in Common Frog Rana temporaria tadpoles: influence of developmental stage, predation risk and social environment. Func Ecolo 13:852–858

Nicol CJ (1995) The social transmission of information and behaviour. Appl Anim Behav Sci 44(2):79–98

Nicolis G, Prigogine I (1977) Self-organization in nonequilibrium systems: from dissipative structures to order through fluctuations. Wiley, New York

Nieh JC (2010) A negative feedback signal that is triggered by peril curbs honey bee recruitment. Curr Biol 20(4):310–315. doi:10.1016/j.cub.2009.12.060

Nisbet ICT (1975) Selective effects of predation in a tern colony. Condor 77:221–226

Niwa HS (1998) School size statistics of fish. J Theor Biol 195(3):351–361

Niwa HS (2003) Power-law versus exponential distributions of animal group sizes. J Theor Biol 224(4):451–457

Niwa HS (2004) Space-irrelevant scaling law for fish school sizes. J Theor Biol 228(3):347–357. doi:10.1016/j.jtbi.2004.01.011

Nocera JJ, Forbes GJ, Giraldeau LA (2006) Inadvertent social information in breeding site selection of natal dispersing birds. Proc Royal Soc London B Biol Sci 273(1584):349–355

Norton GW (1986) Leadership: decision processes of group movement in yellow baboons. In: Else J, Lee P (eds) Primate ecology and conservation. Cambridge University Press, Cambridge, pp 145–156

Nowak MA, Allen B (2015) Inclusive fitness theorizing invokes phenomena that are not relevant for the evolution of eusociality. PLoS Biolo 13:e1002134

Nowak MA, Tarnita CE, Wilson EO (2010) The evolution of eusociality. Nature 466(7310):1057–1062

O'Brien DP (1987) Direct observations of the behavior of Euphausia superba and Euphausia crystallorophias (Crustacea, Euphausiacea) under pack ice during the antarctic spring of 1985. J Crustacean Biol 7:437–448

O'Brien DP (1989) Analysis of the internal arrangement of individuals within crustacean aggregations (Euphausiacea, Mysidacea). J Exper Marine Biolo Ecolo 128(1):1–30. doi:10.1016/0022-0981(89)90090-7

O'Connell CP (1972) Interrelation of biting and filtering in feeding activity of northern anchovy (Engraulis mordax). J Fish Res Board Can 29(3):285

O'Donnell S, Bulova SJ, DeLeon S, Khodak P, Miller S, Sulger E (2015) Distributed cognition and social brains: reductions in mushroom body investment accompanied the origins of sociality in wasps (Hymenoptera: Vespidae). Proc Roy Soc B. doi:10.1098/rspb.2015.0791

O'Donoghue M, Boutin S (1995) Does reproductive synchrony affect juvenile survival rates of northern mammals? Oikos 74:115–121

Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction: the neglected process in evolution, Monographs in population biology. Princeton University Press, Princeton

Ohguchi O (1981) Prey density and selection against oddity by three-spined sticklebacks, Advances in ethology, supplements to journal of comparative ethology. Verlag Paul Parey, Berlin/Hamburg

Okamura B (1986) Group living and the effects of spatial position in aggregations of *Mytilus edulis*. Oecologia 69(3):341–347. doi:10.1007/bf00377054

Okubo A (1986) Dynamical aspects of animal grouping: swarms, schools, flocks, and herds. Adv Biophys 22:1–94

Olsen KH, Grahn M, Lohm J, Langefors A (1998) MHC and kin discrimination in juvenile Arctic charr, Salvelinus alpinus (L.). Anim Behav 56:319–327

Olsen KH, Grahn M, Lohm J (2002) Influence of MHC on sibling discrimination in Arctic char, Salvelinus alpinus (L.). J Chem Ecol 28(4):783–795

Olson RS, Hintze A, Dyer FC, Knoester DB, Adami C (2013) Predator confusion is sufficient to evolve swarming behaviour. J R Soc Interface 10(85):20130305

Olsson M (1994) Rival recognition affects male contest behavior in sand lizards (*Lacerta agilis*). Behav Ecol Sociobiol 35(4):249–252. doi:10.1007/bf00170705

Orpwood JE, Magurran AE, Armstrong JD, Griffiths SW (2008) Minnows and the selfish herd: effects of predation risk on shoaling behaviour are dependent on habitat complexity. Anim Behav 76(1):143–152

Osorno JL, Drummond H (2003) Is obligate siblicidal aggression food sensitive? Behav Ecol Sociobiol 54(6):547–554

Ost M, Jaatinen K, Steele B (2007) Aggressive females seize central positions and show increased vigilance in brood-rearing coalitions of eiders. Anim Behav 73:239–247. doi:10.1016/j.anbehav.2006.04.010

Ostlund-Nilsson S, Mayer I, Huntingford FA (eds) (2006) Biology of the three-spined stickleback. CRC Press, Boca Raton

Ott SR, Rogers SM (2010) Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. Proc Royal Soc B Biol Sci 277:3087–3096

Overath P, Sturm T, Rammensee H-G (2014) Of volatiles and peptides: in search for MHC-dependent olfactory signals in social communication. Cell Mol Life Sci 71(13):2429–2442. doi:10.1007/s00018-014-1559-6

Overdorff DJ, Erhart EM, Mutschler T (2005) Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (Varecia variegata) in southeastern Madagascar? Am J Primatol 66:7–22

Packer C, Pusey AE (1983) Adaptations of female lions to infanticide by incoming males. Am Nat 121:716–728

Packer C, Ruttan L (1988) The evolution of cooperative hunting. Am Nat 132(2):159–198

Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. Am Nat 136:1–19

Packer C, Collins DA, Sindimwo A, Goodall J (1995) Reproductive constraints on aggressive competition in female baboons. Nature 373(6509):60–63. doi:10.1038/373060a0

Palagi E, Dapporto L (2006) Beyond odor discrimination: demonstrating individual recognition by scent in Lemur catta. Chem Senses 31(5):437–443. doi:10.1093/chemse/bjj048

Palestis BG, Burger J (1998) Evidence for social facilitation of preening in the common tern. Anim Behav 56(5):1107–1111

Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim Behav 34(4):1222–1242

Parr AE (1927) A contribution to the theoretical analysis of the schooling behavior of fishes. Occasional papers of the Bingham oceanographic collection

Parrish JK (1989) Re-examining the selfish herd – are central fish safer? Anim Behav 38:1048–1053

Parrish JK, Turchin P (1997) Individual decisions, traffic rules and emergent pattern in schooling fish. In: Parrish JK, Hamner WM (eds) Animal groups in three dimensions. How species aggregate. Cambridge University Press, Cambridge, pp 126–142

Partan S, Marler P (1999) Behavior – communication goes multimodal. Science 283(5406):1272–1273. doi:10.1126/science.283.5406.1272

Partridge BL (1981) Internal dynamics and the interrelations of fish in schools. J Comp Physiol 144(3):313–325

Partridge BL (1982) The structure and function of fish schools. Sci Am 246:114–123

Partridge BL, Pitcher TJ (1980) The sensory basis of fish schools. J Comp Physiol 135:315–325

Partridge BL, Pitcher T, Cullen JM, Wilson J (1980) The 3-dimensional structure of fish schools. Behav Ecol Sociobiol 6(4):277–288. doi:10.1007/bf00292770

Pavlov DS, Kasumyan AO (2000) Patterns and mechanisms of schooling behavior of fish: a review. J Ichthyol 40(Supplement 2):S163–S231

Pellis SM, Pellis VC (1988) Play-fighting in the Syrian golden hamster *Mesocricetus auratus* Waterhouse, and its relationship to serious fighting during postweaning development. Dev Psychobiol 21:323–337

Pellis SM, Pellis VC (1998) Play fighting of rats in comparative perspective: a schema for neurobehavioral analyses. Neurosci Biobehav Rev 23:87–101

Penn D, Potts W (1998) How do major histocompatibility complex genes influence odor and mating preferences? In: Advances in immunology, vol 69. Academic Press Inc, San Diego, pp 411–436

Perez-Barberia FJ, Shultz S, Dunbar RIM (2007) Evidence for coevolution of sociality and relative brain size in three orders of mammals. Evolution 61:2811–2821

Perez-Escudero A, Vicente-Page J, Hinz RC, Arganda S, de Polavieja GG (2014) idTracker: tracking individuals in a group by automatic identification of unmarked animals. Nat Methods 11(7):743. doi:10.1038/nmeth.2994

Perry EF, Manolis JC, Andersen DE (2008) Reduced predation at interior nests in clustered all-purpose territories of least flycatchers (Empidonax minimus). Auk 125(3):643–650. doi:10.1525/auk.2008.07001

Peso M, Richards MH (2010) Knowing who's who: nestmate recognition in the facultatively social carpenter bee, Xylocopa virginica. Anim Behav 79(3):563–570. doi:10.1016/j.anbehav.2009.11.010

Petit DR, Bildstein KL (1987) Effect of group-size and location within the group on the foraging behavior of white ibises. Condor 89(3):602–609. doi:10.2307/1368649

Petit O, Bon R (2010) Decision-making processes: the case of collective movements. Behav Processes 84:635–647

Pettit B, Perna A, Biro D, Sumpter DJT (2013) Interaction rules underlying group decisions in homing pigeons. J R Soc Interface 10:20130529. doi:10.1098/rsif.2013.0529

Pfalzer G, Kusch J (2003) Structure and variability of bat social calls: implications for specificity and individual recognition. J Zool 261:21–33. doi:10.1017/s0952836903003935

Phillips RA, Furness RW, Stewart FM (1998) The influence of territory density on the vulnerability of Arctic skuas Stercorarius parasiticus to predation. Biol Conserv 86(1):21–31. doi:10.1016/s0006-3207(98)00007-x

Pike TW, Laland KN (2010) Conformist learning in nine-spined sticklebacks' foraging decisions. Biol Lett 6(4):466–468. rsbl20091014

Pike TW, Samanta M, Lindström J, Royle NJ (2008) Behavioural phenotype affects social interactions in an animal network. Proce Royal Soc B Biol Sci 275(1650):2515–2520

Piper R (2007) Extraordinary animals: an encyclopaedia of curious and unusual animals. Greenwood Publishing Group, Westport, Connecticut, United States

Pitcher TJ (1973a) 3-dimensional structure of schools in minnow, *Phoxinus phoxinus* (L). Anim Behav 21(NOV):673–686. doi:10.1016/s0003-3472(73)80091-0

Pitcher TJ (1973b) Some field measurements on minnow schools. Trans Am Fish Soc 102(4):840–843. doi:10.1577/1548-8659(1973)102

Pitcher TJ, Parrish JK (1993) The functions of shoaling behavior. In: Pitcher TJ (ed) The behavior of teleost fishes. Chapman & Hall, London, pp 363–439

Pitcher TJ, Partridge BL, Wardle CS (1976) Blind fish can school. Science 194:963–965

Pitcher TJ, Magurran AE, Winfield IJ (1982) Fish in larger shoals find food faster. Behav Ecolo Soc 10:149–151

Piyapong C, Morrell LJ, Croft DP, Dyer JRG, Ioannou CC, Krause J (2007) A cost of leadership in human groups. Ethology 113:821–824

Piyapong C, Butlin RK, Faria JJ, Scruton KJ, Wang J, Krause J (2011) Kin assortment in juvenile shoals in wild guppy populations. Heredity 106(5):749–756

Plath M, Richter S, Tiedemann R, Schlupp I (2008) Male fish deceive competitors about mating preferences. Curr Biol 18(15):1138–1141

Plath M, Richter S, Schlupp I, Tiedemann R (2010) Misleading mollies: surface-but not cave-dwelling Poecilia mexicana males deceive competitors about mating preferences. Acta Ethol 13(1):49–56

Pocklington R, Dill LM (1995) Predation on females or males: who pays for bright male traits? Anim Behav 49(4):1122–1124

Pomeroy H, Heppner F (1992) Structure of turning in airborne rock dove (*Columba livia*) flocks. Auk 109(2):256–267

Popa-Lisseanu AG, Bontadina F, Mora O, Ibanez C (2008) Highly structured fission-fusion societies in an aerial-hawking, carnivorous bat. Anim Behav 75:471–482

Portha S, Deneubourg JL, Detrain C (2002) Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. Behav Ecol 13:776–781

Portugal SJ, Hubel TY, Fritz J, Heese S, Trobe D, Voelkl B, Hailes S, Wilson AM, Usherwood JR (2014) Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. Nature 505(7483):399–402. doi:10.1038/nature12939

Poulin R (2010) Parasite manipulation of host behavior: an update and frequently asked questions. Adv Study Behav 41(41):151–186

Pouyaud L, Desmarais E, Chenuil A, Agnese TF, Bonhomme F (1999) Kin cohesiveness and possible inbreeding in the mouthbrooding tilapia Sarotherodon melanotheron (Pisces Cichlidae). Mol Ecol 8(5):803–812

Pratt SC (2005) Quorum sensing by encounter rates in the ant Temnothorax albipennis. Behav Ecol 16:488–496

Pratt SC, Mallon EB, Sumpter DJT, Franks NR (2002) Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant Leptothorax albipennis. Behav Ecol Sociobiol 52:117–127

Prendergast GS, Zurn CM, Bers AV, Head RM, Hansson LJ, Thomason JC (2008) Field-based video observations of wild barnacle cyprid behaviour in response to textural and chemical settlement cues. Biofouling 24(6):449–459. doi:10.1080/08927010802340135

Price JJ (1999) Recognition of family-specific calls in stripe-backed wrens. Anim Behav 57:483–492. doi:10.1006/anbe.1998.1018

Prins HHT (1996) Ecology and behaviour of the African buffalo, Chapman & Hall wildlife ecology and behaviour series. Springer, Dordrecht

Proops L, McComb K, Reby D (2009) Cross-modal individual recognition in domestic horses (Equus caballus). Proc Natl Acad Sci U S A 106(3):947–951. doi:10.1073/pnas.0809127105

Pugesek BH (1990) Parental effort in the California gull: tests of parent-offspring conflict theory. Behav Ecol Sociobiol 27(3):211–215

Pusey AE (1983) Mother offspring relationships in chimpanzees after weaning. Anim Behav 31:363–377

Queller DC, Strassmann JE (1998) Kin selection and social insects. Bioscience 48:165–175

Quinn JL, Cresswell W (2006) Testing domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. Proc Royal Soc B-Biol Sci 273(1600):2521–2526. doi:10.1098/rspb.2006.3612

Rabøl J, Noer H (1973) Spring migration in the skylark (*Alauda arvensis*) in Denmark. Influence of environmental factors on the flock size and correlation between flock size and migratory direction. Vogelwarte 27:50–65

Rabosky ARD, Corl A, Liwanag HEM, Surget-Groba Y, Sinervo B (2012) Direct fitness correlates and thermal consequences of facultative aggregation in a desert lizard. PLoS One 7(7):e40866. doi:10.1371/journal.pone.0040866

Radakov DV (1973) Schooling in the ecology of fish. John Wiley & Sons, New York

Radford AN (2004) Vocal coordination of group movement by green woodhoopoes (Phoeniculus purpureus). Ethology 110(1):11–20

Radford AN, Du Plessis MA (2003) Bill dimorphism and foraging niche partitioning in the green woodhoopoe. J Anim Ecol 72(2):258–269

Radford AN, Ridley AR (2006) Recruitment calling: a novel form of extended parental care in an altricial species. Curr Biol 16(17):1700–1704

Rajakaruna RS, Brown JA, Kaukinen KH, Miller KM (2006) Major histocompatibility complex and kin discrimination in Atlantic salmon and brook trout. Mol Ecol 15(14):4569–4575. doi:10.1111/j.1365-294X.2006.03113.x

Ramos-Fernandez G, Boyer D, Gomez VP (2006) A complex social structure with fission-fusion properties can emerge from a simple foraging model. Behav Ecol Sociobiol 60:536–549

Ramseyer A, Boissy A, Dumont B, Thierry B (2009a) Decision making in group departures of sheep is a continuous process. Anim Behav 78:71–78

Ramseyer A, Thierry B, Boissy A, Dumont B (2009b) Decision-making processes in group departures of cattle. Ethology 115:948–957

Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA (2003) Spontaneous emergence of leaders and followers in foraging pairs. Nature 423:432–434

Rands SA, Pettifor RA, Rowcliffe JM, Cowlishaw G (2006) Social foraging and dominance relationships: the effects of socially mediated interference. Behav Ecol Sociobiol 60(4):572–581. doi:10.1007/s00265-006-0202-4

Rangel J, Seeley TD (2012) Colony fissioning in honey bees: size and significance of the swarm fraction. Insect Soc 59:453–462

Rangel J, Reeve HK, Seeley TD (2013) Optimal colony fissioning in social insects: testing an inclusive fitness model with honey bees. Insect Soc 60:445–452

Rao D (2009) Experimental evidence for the amelioration of shadow competition in an orb web spider through the ‘Ricochet’ effect. Ethology 115(7):691–697

Rashevsky N (1951) A note on imitative behavior and information. Bull Math Biophys 13:147–151

Ratchford SG, Eggleston DB (1998) Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. Anim Behav 56:1027–1034

Ratcliffe JM, ter Hofstede HM (2005) Roosts as information centres: social learning of food preferences in bats. Biol Lett 1(1):72–74

Ratti O, Ojanen U, Helle P (2006) Increasing group size dilutes black fly attack rate in Black Grouse. Ornis Fennica 83:86–90

Rayor LS, Uetz GW (1990) Trade-offs in foraging success and predation risk with spatial position in colonial spiders. Behav Ecol Sociobiol 27(2):77–85. doi:10.1007/bf00168449

Rayor LS, Uetz GW (1993) Ontogenic shifts within the selfish herd – predation risk and foraging trade-offs change with age in colonial web-building spiders. Oecologia 95(1):1–8

Reader SM, Laland KN (eds) (2003) Animal innovation, vol 10. Oxford University Press, Oxford

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82(2):291–318

Reebs SG (2000) Can a minority of informed leaders determine the foraging movements of a fish shoal? Anim Behav 59:403–409

Reebs SG (2001) Influence of body size on leadership in shoals of golden shiners, Notemigonus crysoleucas. Behaviour 138:797–809

Reebs SG, Saulnier N (1997) The effect of hunger on shoal choice in golden shiners (Pisces: Cyprinidae, Notemigonus crysoleucas). Ethology 103(8):642–652

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133(3):407–435. doi:10.1086/284926

Reid CR, Sumpter DJT, Beekman M (2011) Optimisation in a natural system: argentine ants solve the Towers of Hanoi. J Exp Biol 214(1):50–58. doi:10.1242/jeb.048173

Rendell LE, Whitehead H (2003) Vocal clans in sperm whales (Physeter macrocephalus). Proc Royal Soc B-Biol Sci 270:225–231

Rendell L, Fogarty L, Hoppitt WJ, Morgan TJ, Webster MM, Laland KN (2011) Cognitive culture: theoretical and empirical insights into social learning strategies. Trends Cogn Sci 15(2):68–76

Reuter H, Breckling B (1994) Selforganization of fish schools – an object-oriented model. Ecol Model 75:147–159. doi:10.1016/0304-3800(94)90014-0

Reynolds CW (1987) Flocks, herds, and schools: a distributed behavioral model. Comput Graph 21:25–34

Reznick DA, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. Nature 346:357–359

Richner H, Heeb P (1995) Is the information center hypothesis a flop? Adv Study Behav 24:1–45

Riehl C (2006) Widespread cannibalism by fledglings in a nesting colony of Black-crowned Night-herons. Wilson J Ornithol 118(1):101–104

Rieucau G, Giraldeau LA (2009) Persuasive companions can be wrong: the use of misleading social information in nutmeg mannikins. Behav Ecol 20:1217–1222

Rifkin JL, Nunn CL, Garamszegi LZ (2012) Do animals living in larger groups experience greater parasitism? A meta-analysis. Am Nat 180:70–82

Riley JR, Greggers U, Smith AD, Reynolds DR, Menzel R (2005) The flight paths of honeybees recruited by the waggle dance. Nature 435(7039):205–207

Rippin AB, Boag DA (1974) Spacial organization among male sharp-tailed grouse on arenas. Can J Zool 52(5):591–597

Ritz DA (2000) Is social aggregation in aquatic crustaceans a strategy to conserve energy? Can J Fish Aquat Sci 57:59–67

Ritz DA, Hobday AJ, Montgomery JC, Ward AJW (2011) Social aggregation in the pelagic zone with special reference to fish and invertebrates. In: Lesser M (ed) Advances in marine biology, vol 60, Vol., pp 161–227

Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51(5):1077–1086

Robinson EJH, Jackson DE, Holcombe M, Ratnieks FLW (2005) Insect communication – 'no entry' signal in ant foraging. Nature 438(7067):442–442. doi:10.1038/438442a

Robinson EJH, Franks NR, Ellis S, Okuda S, Marshall JAR (2011) A simple threshold rule is sufficient to explain sophisticated collective decision-making. Plos One 6(5):e19981

Robisson P, Aubin T, Bremond JC (1993) Individuality in the voice of the emperor penguin aptenodytes-forsteri – adaptation to a noisy environment. Ethology 94(4):279–290

Roche EA, Brown CR, Brown MB (2011) Heritable choice of colony size in cliff swallows: does experience trump genetics in older birds? Anim Behav 82(6):1275–1285

Rode NO, Lievens EJP, Flaven E, Segard A, Jabbour-Zahab R, Sanchez MI, Lenormand T (2013) Why join groups? Lessons from parasite-manipulated Artemia. Ecol Lett 16:493–501

Rohwer S, Ewald PW (1981) The cost of dominance and advantage of subordination in a badge signaling system. Evolution 35(3):441–454. doi:10.2307/2408193

Romanczuk P, Couzin ID, Schimansky-Geier L (2009) Collective motion due to individual escape and pursuit response. Phys Rev Lett 102(1):010602. doi:10.1103/PhysRevLett.102.010602

Romey WL (1995) Position preferences within groups – do whirligigs select positions which balance feeding opportunities with predator avoidance. Behav Ecol Sociobiol 37(3):195–200. doi:10.1007/bf00176717

Romey WL (1996) Individual differences make a difference in the trajectories of simulated fish schools. Ecol Model 92:65–77

Romey WL, Galbraith E (2008) Optimal group positioning after a predator attack: the influence of speed, sex, and satiation within mobile whirligig swarms. Behav Ecol 19(2):338–343. doi:10.1093/beheco/arm138

Romey WL, LaBuda S (2010) Predator type, not body condition, influences positioning within whirligig groups. Behav Ecol Sociobiol 64(4):665–673. doi:10.1007/s00265-009-0884-5

Romey WL, Wallace AC (2007) Sex and the selfish herd: sexual segregation within nonmating whirligig groups. Behav Ecol 18(5):910–915. doi:10.1093/beheco/arm057

Romey WL, Walston AR, Watt PJ (2008) Do 3-D predators attack the margins of 2-D selfish herds? Behav Ecol 19(1):74–78. doi:10.1093/beheco/arm105

Romey WL, Miller MM, Vidal JM (2014) Collision avoidance during group evasive manoeuvres: a comparison of real versus simulated swarms with manipulated vision and surface wave detectors. Proc Royal Soc B-Biol Sci 281(1788):20140812. doi:10.1098/rspb.2014.0812

Romilio A, Salisbury SW (2011) A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity. Cretaceous Res 32(2):135–142

Rosengaus RB, Guldin MR, Traniello JF (1998a) Inhibitory effect of termite fecal pellets on fungal spore germination. J Chem Ecol 24(10):1697–1706

Rosengaus RB, Maxmen AB, Coates LE, Traniello JF (1998b) Disease resistance: a benefit of sociality in the dampwood termite Zootermopsis angusticollis (Isoptera: Termopsidae). Behav Ecol Sociobiol 44(2):125–134

Rosengaus RB, Lefebvre ML, Traniello JF (2000a) Inhibition of fungal spore germination by Nasutitermes: evidence for a possible antiseptic role of soldier defensive secretions. J Chem Ecol 26(1):21–39

Rosengaus RB, Traniello JFA, Lefebvre ML, Carlock DM (2000b) The social transmission of disease between adult male and female reproductives of the dampwood termite Zootermopsis angusticollis. Ethol Ecol Evol 12(4):419–433

Rosenthal SB, Twomey CR, Hartnett AT, Wu HS, Couzin ID (2015) Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. Proc Natl Acad Sci U S A 112:4690–4695

Roskaft E, Jarvi T, Bakken M, Bech C, Reinertsen RE (1986) The relationship between social-status and resting metabolic-rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Anim Behav 34:838–842. doi:10.1016/s0003-3472(86)80069-0

Roth LM, Willis ER (1960) The biotic associations of cockroaches. Smithsonian Misc Coll 141:1–470

Rowcliffe JM, Pettifor RA, Carbone C (2004) Foraging inequalities in large groups: quantifying depletion experienced by individuals in goose flocks. J Anim Ecol 73(1):97–108. doi:10.1111/j.1365-2656.2004.00783.x

Rubenstein DI, Hack M (2004) Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In: Kappeler PP, VSC (Eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, Cambridge, pp. 266–279

Ruch J, Heinrich L, Bilde T, Schneider JM (2009) Relatedness facilitates cooperation in the subsocial spider, Stegodyphus tentoriicola. Bmc Evol Biol 9:257. doi:10.1186/1471-2148-9-257

Ruch J, Herberstein ME, Schneider JM (2014) Families hunt more successfully: effect of group composition on hunting and communal feeding. Anim Behav 91:171–178. doi:10.1016/j.anbehav.2014.03.013

Rutz C (2012) Predator fitness increases with selectivity for odd prey. Curr Biol 22(9):820–824

Ryan CME, Lea SEG (1994) Images of conspecifics as categories to be discriminated by pigeons and chickens – slides, video tapes, stuffed birds and live birds. Behav Processes 33(1–2):155–175. doi:10.1016/0376-6357(94)90064-7

Rybak F, Sureau G, Aubin T (2002) Functional coupling of acoustic and chemical signals in the courtship behaviour of the male Drosophila melanogaster. Proc Royal Soc B-Biol Sci 269(1492):695–701. doi:10.1098/rspb.2001.1919

Ryder TB, Blake JG, Loiselle BA (2006) A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. Auk 123(1):247–258

Ryer CH, Olla BL (1995) Influences of food distribution on fish foraging behaviour. Anim Behav 49(2):411–418

Sachser N, Kaiser S (2010) The social modulation of behavioural development. In: Kappeler P (ed) Animal behaviour: evolution and mechanisms. Springer, Berlin/London/New York, pp 505–536

Sahin E (2005) Swarm robotics: from sources of inspiration to domains of application. In: Swarm robotics. Springer, Heidelberg, pp 10–20

Saif M, Chatterjee D, Buske C, Gerlai R (2013) Sight of conspecific images induces changes in neurochemistry in zebrafish. Behav Brain Res 243:294–299. doi:10.1016/j.bbr.2013.01.020

Sandem AI, Janczak AM, Salte R, Brotastad BO (2006) The use of diazepam as a pharmacological validation of eye white as an indicator of emotional state in dairy cows. Appl Anim Behav Sci 96(3–4):177–183. doi:10.1016/j/applanim.2005.06.008

Sasaki T, Granovskiy B, Mann RP, Sumpter DJT, Pratt SC (2013) Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. Proc Natl Acad Sci U S A 110:13769–13773

Satischandra SHK, Kudavidanage EP, Kotagama SW, Goodale EBEN (2007) The benefits of joining mixed-species flocks for greater racket-tailed drongos *Dicrurus paradiseus*. Forktail 23:145

Sayigh LS, Tyack PL, Wells RS, Solow AR, Scott MD, Irvine AB (1999) Individual recognition in wild bottlenose dolphins: a field test using playback experiments. Anim Behav 57:41–50. doi:10.1006/anbe.1998.0961

Schaller GB (1972) The Serengeti lion. University of Chicago Press, Chicago

Schino G (2001) Grooming, competition and social rank among female primates: a meta-analysis. Anim Behav 62(2):265–271

Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1988) Allogrooming as a tension reduction mechanism: a behavioral approach. Am J Primatol 16(1):43–50

Schneider KJ (1984) Dominance, predation, and optimal foraging in white-thorated sparrow flocks. Ecology 65(6):1820–1827. doi:10.2307/1937778

Schorger AW (1955) The passenger pigeon: its natural history and extinction. University of Oklahoma, Oklahoma, USA

Schultz KM, Passino KM, Seeley TD (2008) The mechanism of flight guidance in honeybee swarms: subtle guides or streaker bees? J Exp Biol 211:3287–3295

Seeley TD (1995) The wisdom of the hive. Harvard University Press, Cambridge

Seeley TD (2002) When is self-organization used in biological systems? Biol Bull 202(3):314–318. doi:10.2307/1543484

Seeley, TD, (2009). The wisdom of the hive: the social physiology of honey bee colonies. Harvard University Press.

Seeley TD (2010) Honeybee democracy. Princeton University Press, Princeton, NJ, USA

Seeley TD, Towne WF (1992) Tactics of dance choice in honey-bees – do foragers compare dances. Behav Ecol Sociobiol 30:59–69

Seeley TD, Visscher PK (2003) Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. Behav Ecol Sociobiol 54:511–520

Seeley TD, Visscher PK (2004) Quorum sensing during nest-site selection by honeybee swarms. Behav Ecol Sociobiol 56:594–601

Seeley TD, Visscher PK (2008) Sensory coding of nest-site value in honeybee swarms. J Exp Biol 211:3691–3697

Seeley TD, Mikheyev AS, Pagano GJ (2000) Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. J Comp Physiol A 186(9):813–819

Seeley TD, Visscher PK, Schlegel T, Hogan PM, Franks NR, Marshall JAR (2012) Stop signals provide cross inhibition in collective decision-making by Honeybee Swarms. Science 335:108–111

Selman J, Goss-Custard JD (1988) Interference between foraging redshank Tringa totanus. Anim Behav 36(5):1542–1544

Seltmann A, Majolo B, Schulke O, Ostner J (2013) The organization of collective group movements in Wild Barbary Macaques (Macaca sylvanus): social structure drives processes of group coordination in Macaques. Plos One 8:e67285

Senar JC, Camerino M, Metcalfe NB (1990) Familiarity breeds tolerance – the development of social stability in flocking siskins (*Carduelis spinus*). Ethology 85(1):13–24

Sendova-Franks AB, Franks NR (1999) Self-assembly, self-organization and division of labour. Philos Trans Royal Soc B-Biol Sci 354(1388):1395–1405. doi:10.1098/rstb.1999.0487

Seppa T, Laurila A, Peuhkuri N, Piironen J, Lower N (2001) Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles. Can J Fish Aquat Sci 58(7):1380–1385

Seppala O, Karvonen A, Valtonen ET (2008) Shoaling behaviour of fish under parasitism and predation risk. Anim Behav 75:145–150

Serrano D, Tella JL (2007) The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. Am Nat 169(2):E53–E67

Serrano D, Forero MG, Donazar JA, Tella JL (2004) Dispersal and social attraction affect colony selection and dynamics of lesser kestrels. Ecology 85(12):3438–3447. doi:10.1890/04-0463

Serrano D, Oro D, Ursua E, Tella JL (2005) Colony size selection determines adult survival and dispersal preferences: allee effects in a colonial bird. Am Nat 166(2):E22–E31. doi:10.1086/431255

Shang YL, Bouffanais R (2014) Influence of the number of topologically interacting neighbors on swarm dynamics. Sci Rep 4:4184. doi:10.1038/srep04184

Shapiro PN, Penrod S (1986) Metaanalysis of facial identification studies. Psychol Bull 100(2):139–156. doi:10.1037/0033-2909.100.2.139

Sheehan MJ, Tibbetts EA (2011) Specialized face learning is associated with individual recognition in paper wasps. Science 334(6060):1272–1275. doi:10.1126/science.1211334

Sheehan and Tibbetts 2008. Robust longterm social memories in a paper wasp. Current Biology 18 R851–R852

Sherman PW, Holmes WG (1985) Kin recognition – issues and evidence. In: Hölldobler B, Lindauer M (eds) Experimental behavioral ecology and sociobiology. Sinauer Associates, Mass., pp 437–460

Sherman PW, Reeve HK, Pfennig DW (1997) Recognition systems. In: Krebs JR, Davies NB (eds) Behavioural ecology, 4th edn. Blackwell, Oxford

Shultz S, Opie C, Atkinson QD (2011) Stepwise evolution of stable sociality in primates. Nature 479(7372):219–222

Sibly RM (1983) Optimal group size is unstable. Anim Behav 31(3):947–948

Siegfried WR, Underhill LG (1975) Flocking as an anti-predator strategy in doves. Anim Behav 23:504–508

Sih A, Bell AM, Johnson JC, Ziemba RE (2004a) Behavioral syndromes: an integrative overview. Q Rev Biol 79(3):241–277

Sih A, Bell A, Johnson JC (2004b) Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19(7):372–378

Sih A, Mathot KJ, Moiron M, Montiglio PO, Wolf M, Dingemanse NJ (2015) Animal personality and state-behaviour feedbacks: a review and guide for empiricists. Trends Ecol Evol 30:50–60

Silk MJ, Croft DP, Tregenza T, Bearhop S (2014) The importance of fission-fusion social group dynamics in birds. Ibis 156:701–715

Simons AM (2004) Many wrongs: the advantage of group navigation. Trends Ecol Evol 19:453–455

Simpson SJ, McCaffery AR, Hagele BF (1999) A behavioural analysis of phase change in the desert locust. Biol Rev Camb Philos Soc 74:461–480

Simpson SJ, Sword GA, Lorch PD, Couzin ID (2006) Cannibal crickets on a forced march for protein and salt. Proc Natl Acad Sci U S A 103(11):4152–4156. doi:10.1073/pnas.0508915103

Sinclair ARE (1977) The African buffalo: a study of resource limitation of populations. University of Chicago Press, Chicago

Sinclair AR (1985) Does interspecific competition or predation shape the African ungulate community? J Anim Ecol 54:899–918

Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF (2000) Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. Horm Behav 38:222–233

Sinervo B, Chaine A, Clobertt J, Calsbeek R, Hazard L, Lancaster L, McAdam AG, Alonzo S, Corrigan G, Hochberg ME (2006) Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. Proc Natl Acad Sci U S A 103(19):7372–7377. doi:10.1073/pnas.0510260103

Singer TL (1998) Roles of hydrocarbons in the recognition systems of insects. Am Zool 38(2):394–405

Skogland T (1989) Natural-selection of wild reindeer life-history traits by food limitation and predation. Oikos 55:101–110

Slaa EJ, Wassenberg J, Biesmeijer JC (2003) The use of field–based social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. Ecol Entomol 28(3):369–379

Slotow R, Rothstein SI (1995) Influence of social status, distance from cover, and group size on feeding and vigilance in white-crowned Sparrows. Auk 112(4):1024–1031

Smith GW, Glass CW, Johnstone ADF, Mojsiewicz WR (1993) Diurnal patterns in the spatial relationships between saithe, Pullachius virens, schooling in the wild. J Fish Biol 43(suppl A):315–325

Soma KK, Wingfield JC (2001) Dehydroepiandrosterone in songbird plasma: seasonal regulation and relationship to territorial aggression. Gen Comp Endocrinol 123:144–155

Soria M, Freon P, Chabanet P (2007) Schooling properties of an obligate and a facultative fish species. J Fish Biol 71(5):1257–1269. doi:10.1111/j.1095-8649.2007.01554.x

Spehar SN, Di Fiore A (2013) Loud calls as a mechanism of social coordination in a fission-fusion taxon, the white-bellied spider monkey (Ateles belzebuth). Behav Ecol Sociobiol 67(6):947–961. doi:10.1007/s00265-013-1520-y

Spence R, Smith C (2007) The role of early learning in determining shoaling preferences based on visual cues in the zebrafish, Danio rerio. Ethology 113(1):62–67

Sperry TS, Wingfield JC (2003) Serotonergic regulation of glucocorticoid release in male white-crowned sparrows. Integr Comp Biol 43:925

Sridhar H, Beauchamp G, Shanker K (2009) Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Anim Behav 78(2):337–347

Stamhuis EJ, Reede-Dekker T, Van Etten Y, De Wiljes JJ, Videler JJ (1996) Behaviour and time allocation of the burrowing shrimp *Callianassa subterranea* (Decapoda, Thalassinidea). J Exp Mar Biol Ecol 204(1):225–239

Stander PE (1992) Cooperative hunting in lions: the role of the individual. Behav Ecol Sociobiol 29(6):445–454

Steele WK, Hockey PA (1995) Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (*Larus dominicanus*). Auk 112:847–859

Steiger S, Mueller JK (2008) 'True' and 'untrue' individual recognition: suggestion of a less restrictive definition. Trends Ecol Evol 23(7):355. doi:10.1016/j.tree.2008.01.014

Stensland EVA, Angerbjörn A, Berggren PER (2003) Mixed species groups in mammals. Mamm Rev 33(3–4):205–223

Stephens DW, Anderson JP, Benson KE (1997) On the spurious occurrence of Tit for Tat in pairs of predator-approaching fish. Anim Behav 53(1):113–131

Stewart KJ, Harcourt AH (1994) Gorillas vocalizations during rest periods – signals of impending departure. Behaviour 130:29–40

Stillman RA, Deutsch JC, Clutton-Brock TH, Sutherland WJ (1996) Black hole models of ungulate lek size and distribution. Anim Behav 52(5):891–902

Stillman RA, Goss-Custard JD, Alexander MJ (2000) Predator search pattern and the strength of interference through prey depression. Behav Ecol 11(6):597–605

Stoddard PK, Kilburn MD, Patterson KH (1996) Complex electric signal structure in reproducing gymnotiform electric fish. Soc Neurosci Abstr 22(1–3):450

Strandburg-Peshkin A, Twomey CR, Bode NWF, Kao AB, Katz Y, Ioannou CC, Rosenthal SB, Torney CJ, Wu HS, Levin SA, Couzin ID (2013) Visual sensory networks and effective information transfer in animal groups. Curr Biol 23(17):R709–R711. doi:10.1016/j.cub.2013.07.059

Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC (2015) Shared decision-making drives collective movement in wild baboons. Science 348:1358–1361

Strassmann JE, Klingler CJ, Arevalo E, Zacchi F, Husain A, Williams J, Seppa P, Queller DC (1997) Absence of within-colony kin discrimination in behavioural interactions of swarm-founding-wasps. Proc Royal Soc B-Biol Sci 264(1388):1565–1570

Strassmann JE, Page RE Jr, Robinson GE, Seeley TD (2011) Kin selection and eusociality. Nature 471(7339):E5–E6

Strodl MA, Schausberger P (2012) Social familiarity modulates group living and foraging behaviour of juvenile predatory mites. Naturwissenschaften 99(4):303–311. doi:10.1007/s00114-012-0903-7

Strodl MA, Schausberger P (2013) Social familiarity relaxes the constraints of limited attention and enhances reproduction of group-living predatory mites. Oikos 122(8):1217–1226. doi:10.1111/j.1600-0706.2012.20833.x

Strömbom D (2011) Collective motion from local attraction. J Theor Biol 283(1):145–151. doi:10.1016/j.jtbi.2011.05.019

Strömbom D, Mann RP, Wilson AM, Hailes S, Morton AJ, Sumpter DJ, King AJ (2014) Solving the shepherding problem: heuristics for herding autonomous, interacting agents. J R Soc Interface 11(100):20140719

Stumbo AD, James CT, Goater CP, Wisenden BD (2012) Shoaling as an antiparasite defence in minnows (Pimephales promelas) exposed to trematode cercariae. J Anim Ecol 81(6):1319–1326. doi:10.1111/j.1365-2656.2012.02012.x

Sturdy CB, Phillmore LS, Sartor JJ, Weisman RG (2001) Reduced social contact causes auditory perceptual deficits in zebra finches, Taeniopygia guttata. Anim Behav 62:1207–1218. doi:10.1006/anbe.2001.1864

Sturm T, Leinders-Zufall T, Macek B, Walzer M, Jung S, Pommerl B, Stevanovic S, Zufall F, Overath P, Rammensee HG (2013) Mouse urinary peptides provide a molecular basis for genotype discrimination by nasal sensory neurons. Nat Commun 4:1616. doi:10.1038/ncomms2610

Sueur C, Petit O (2008a) Organization of group members at departure is driven by social structure in Macaca. Int J Primatol 29:1085–1098

Sueur C, Petit O (2008b) Shared or unshared consensus decision in macaques? Behav Processes 78:84–92

Sueur C, Petit O, Deneubourg JL (2009) Selective mimetism at departure in collective movements of Macaca tonkeana: an experimental and theoretical approach. Anim Behav 78:1087–1095

Sueur C, Petit O, De Marco A, Jacobs AT, Watanabe K, Thierry B (2011a) A comparative network analysis of social style in macaques. Anim Behav 82(4):845–852. doi:10.1016/j.anbehav.2011.07.020

Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D, Aureli F (2011b) Collective decision-making and fission-fusion dynamics: a conceptual framework. Oikos 120:1608–1617

Sueur C, MacIntosh AJJ, Jacobs AT, Watanabe K, Petit O (2013) Predicting leadership using nutrient requirements and dominance rank of group members. Behav Ecol Sociobiol 67:457–470

Sugden LG, Beyersbergen GW (1986) Effect of density and concealment on American crow predation of simulated duck nests. J Wildl Manag 50:9–14

Sullivan KA (1984) Information exploitation by downy woodpeckers in mixed-species flocks. Behaviour 91(4):294–311

Sumpter DJT (2010) Collective animal behaviour. Princeton University Press, Princeton and Oxford

Sumpter DJT, Pratt SC (2009) Quorum responses and consensus decision making. Philos Trans Royal Soc B-Biol Sci 364:743–753

Sumpter DJT, Mann RP, Perna A (2012) The modelling cycle for collective animal behaviour. Interface Focus 2(6):764–773. doi:10.1098/rsfs.2012.0031

Svendsen JC, Skov J, Bildsoe M, Steffensen JF (2003) Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions. J Fish Biol 62(4):834–846. doi:10.1046/j.1095-8649.2003.00068.x

Swain DT, Couzin ID, Leonard NE (2015) Coordinated speed oscillations in schooling killifish enrich social communication. J Nonlinear Sci 25(5):1077–1109

Swaney W, Kendal J, Capon H, Brown C, Laland KN (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. Anim Behav 62:591–598

Sword GA, Simpson SJ, El Hadi OTM, Wilps H (2000) Density-dependent aposematism in the desert locust. Proc Royal Soc B-Biol Sci 267:63–68

Symington MM (1990) Fission-fusion social-organization in ateles and pan. Int J Primatol 11:47–61

Taborsky B, Oliveira RF (2012) Social competence: an evolutionary approach. Trends Ecol Evol 27:679–688

Tanabe Y, Nakamura T, Fujioka K, Doi O (1979) Production and secretion of sex steroid-hormones by the testes, the ovary, and the adrenal-glands of embryonic and young chickens (*Gallus domesticus*). Gen Comp Endocrinol 39:26–33

Tanaka S, Maeno K (2010) A review of maternal and embryonic control of phase-dependent progeny characteristics in the desert locust. J Insect Physiol 56:911–918

Tarling GA, Klevjer T, Fielding S, Watkins J, Atkinson A, Murphy E, Korb R, Whitehouse M, Leaper R (2009) Variability and predictability of Antarctic krill swarm structure. Deep Sea Res Part I: Oceanograph Res Pap 56(11):1994–2012

Tate AJ, Fischer H, Leigh AE, Kendrick KM (2006) Behavioural and neurophysiological evidence for face identity and face emotion processing in animals. Philos Trans Royal Soc B-Biol Sci 361(1476):2155–2172. doi:10.1098/rstb.2006.1937

Taylor RJ (1984) Predation. Chapman and Hall, New York

Ten Eyck GR (2008) Serotonin modulates vocalizations and territorial behavior in an amphibian. Behav Brain Res 193:144–147

Tenaza R (1971) Behavior and nesting success relative to nest location in adelie penguins (*Pygoscelis adeliae*). Condor 73(1):81. doi:10.2307/1366127

Theis KR, Venkataraman A, Dycus JA, Koonter KD, Schmitt-Matzen EN, Wagner AP, Holekamp KE, Schmidt TM (2013) Symbiotic bacteria appear to mediate hyena social odors. Proc Natl Acad Sci U S A 110(49):19832–19837. doi:10.1073/pnas.1306477110

Theodorakis CW (1989) Size segregation and the effects of oddity on predation risk in minnow schools. Anim Behav 38(3):496–502

Thiebault A, Mullers RH, Pistorius PA, Tremblay Y (2014) Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. Behav Ecolo 25(6):1302–1310

Thorpe WH (1956) Learning and instinct in animals. Methuen, London

Thulborn RA, Wade M (1979) Dinosaur stampede in the Cretaceous of Queensland. Lethaia 12(3):275–279

Tibbetts EA (2002) Visual signals of individual identity in the wasp Polistes fuscatus. Proc Royal Soc B Biolo Sci 269(1499):1423–1428. doi:10.1098/rspb.2002.2031

Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22(10):529–537. doi:10.1016/j.tree.2007.09.001

Tibbetts EA, Lindsay R (2008) Visual signals of status and rival assessment in Polistes dominulus paper wasps. Biol Lett 4(3):237–239. doi:10.1098/rsbl.2008.0048

Tinbergen N (1951) The study of instinct. Oxford University Press, Oxford

Tinbergen N (1963) On aims and methods of ethology. Z Tierpsychol 20:410–433

Tinbergen N, Impekoven M, Franck D (1967) An experiment on spacing-out as a defence against predation. Behaviour 28(3):307–320

Tosh CR, Jackson AL, Ruxton GD (2006) The confusion effect in predatory neural networks. Am Nat 167(2):E52–E65

Tóth Z, Bókony V, Lendvai ÁZ, Szabó K, Pénzes Z, Liker A (2009) Effects of relatedness on social-foraging tactic use in house sparrows. Anim Behav 77(2):337–342

Trainor BC, Sisk CL, Nelson RJ (2009) Hormones and the development and expression of aggressive behavior. In: Pfaff DW, Arnold AP, Etgen AM, Fahrbach SE, Rubin RT (eds) Hormones brain and behavior. Academic Press, Amsterdam, pp 167–203

Traniello JF, Rosengaus RB, Savoie K (2002) The development of immunity in a social insect: evidence for the group facilitation of disease resistance. Proc Natl Acad Sci 99(10):6838–6842

Treherne JE, Foster WA (1981) Group transmission of predator avoidance-behavior in a marine insect – the Trafalgar Effect. Anim Behav 29:911–917

Treisman M (1975a) Predation and evolution of gregariousness.1. Models for concealment and evasion. Anim Behav 23:779–800

Treisman M (1975b) Predation and evolution of gregariousness.2. Economic model for predator–prey interaction. Anim Behav 23:801–825

Trivers RL (1971) The evolution of reciprocal altruism. Quar Rev Biolo 46:35–57

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871–1971. Aldine, Chicago, pp 136–179

Trivers RL (1974) Parent-offspring conflict. Am Zool 14(1):249–264

Trokovic N, Gonda A, Herczeg G, Laurila A, Merila J (2011) Brain plasticity over the metamorphic boundary: carry-over effect of larval environment on froglet brain development. J Evol Biol 24:1380–1385

Tsubaki Y (1981) Some beneficial effects of aggregation in young larvae of Pryeria sinica Moore (Lepidoptera: Zygaenidae). Res Popul Ecol 23(1):156–167

Tucker JK, Paukstis GL, Janzen FJ (2008) Does predator swamping promote synchronous emergence of turtle hatchlings among nests? Behav Ecolo 19(1):35–40

Tunstrom K, Katz Y, Ioannou CC, Huepe C, Lutz MJ, Couzin ID (2013) Collective states, multistability and transitional behavior in schooling fish. Plos Comp Biolo 9(2). doi:10.1371/journal.pcbi.1002915

Turner GF, Pitcher TJ (1986) Attack abatement: a model for group protection by combined avoidance and dilution. Am Natu 128:228–240

Uetz GW, Roberts JA (2002) Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. Brain Behav Evol 59(4):222–230

Usherwood JR, Stavrou M, Lowe JC, Roskilly K, Wilson AM (2011) Flying in a flock comes at a cost in pigeons. Nature 474(7352):494–497. doi:10.1038/nature10164

Utne-Palm AC, Hart PJB (2000) The effects of familiarity on competitive interactions between threespined sticklebacks. Oikos 91(2):225–232

Uvarov BP (1977) Grasshoppers and locusts: a handbook of general acridology, vol 2. Centre for Overseas Pest Research, London

Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. Phil Trans Royal Soc B Biolo Sci 357(1427):1549–1557

Van der Velden J, Zheng Y, Patullo BW, Macmillan DL (2008) Crayfish recognize the faces of fight opponents. Plos One 3(2). doi:10.1371/journal.pone.0001695

Van Dyk DA, Evans CS (2007) Familiar-unfamiliar discrimination based on visual cues in the Jacky dragon, Amphibolurus muricatus. Anim Behav 74:33–44. doi:10.1016/j.anbehav.2006.06.018

van Leeuwen EJC, Mulenga IC, Chidester DL (2014) Early social deprivation negatively affects social skill acquisition in chimpanzees (Pan troglodytes). Anim Cogn 17:407–414

van Oers K, Drent PJ, De Goede P, Van Noordwijk AJ (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc Royal Soc London Series B Biolo Sci 271(1534):65–73

Van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87(1):120–144

Van Valkenburgh B, Maddox T, Funston PJ, Mills MG, Grether GF, Carbone C (2009) Sociality in Rancho La Brea Smilodon: arguments favour 'evidence' over 'coincidence'. Biol Lett 5(4):563–564

van Zweden JS, D'Ettorre G (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, New York, pp 222–243

Vehrencamp SL (1978) The adaptive significance of communal nesting in groove-billed anis (Crotophaga sulcirostris). Behav Ecol Sociobiol 4(1):1–33

Vehrencamp SL (1983) Optimal degree of skew in cooperative societies. Am Zool 23(2):327–335

Veissier I, Leneindre P, Garel JP (1990) Decrease in cow-calf attachment after weaning. Behav Processes 21:95–105

Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA (1991) Producers, scroungers, and group foraging. Am Natu 137:847–863

Vicsek T, Czirok A, Benjacob E, Cohen I, Shochet O (1995) Novel type of phase-transition in a system of self-driven particles. Phys Rev Lett 75(6):1226–1229. doi:10.1103/PhysRevLett.75.1226

Viscido SV, Wethey DS (2002) Quantitative analysis of fiddler crab flock movement: evidence for 'selfish herd' behaviour. Anim Behav 63:735–741. doi:10.1006/anbe.2001.1935

Viscido SV, Parrish JK, Grunbaum D (2004) Individual behavior and emergent properties of fish schools: a comparison of observation and theory. Mar Ecol Prog Ser 273:239–249. doi:10.3354/meps273239

Viscido SV, Parrish JK, Grunbaum D (2005) The effect of population size and number of influential neighbors on the emergent properties of fish schools. Ecol Model 183(2–3):347–363. doi:10.1016/j.ecolmodel.2004.08.019

Visser IN, Smith TG, Bullock ID, Green GD, Carlsson OG, Imberti S (2008) Antarctic peninsula killer whales (Orcinus orca) hunt seals and a penguin on floating ice. Mar Mamm Sci 24(1):225–234

Vital C, Martins EP (2009) Using graph theory metrics to infer information flow through Animal Social Groups: a computer simulation analysis. Etholo 115:347–355

Vitone ND, Altizer S, Nunn CL (2004) Body size, diet and sociality influence the species richness of parasitic worms in anthropoid primates. Evolu Ecolo Res 6(2):183–199

Voelkl B, Portugal SJ, Unsöld M, Usherwood JR, Wilson AM, Fritz J (2015) Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis. Proc Natl Acad Sci 112(7):2115–2120. doi:10.1073/pnas.1413589112

von Frisch KR (1967) The dance language and orientation of bees. Harvard University Press, Cambridge, MA

Waldman B, Adler K (1979) Toad tadpoles associate preferentially with siblings. Nature 282(5739):611–613. doi:10.1038/282611a0

Walker SE, Marshall SD, Rypstra AL, Taylor DH (1999) The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). Anim Behav 58:515–520. doi:10.1006/anbe.1999.1180

Wallraff HG (1978) Social interrelations involved in migratory orientation of birds – possible contribution of field studies. Oikos 30:401–404

Walser ES, Hague P, Yeomans M (1983) Preferences for sibling or mother in dalesbred and jacob twin lambs. Appl Anim Etholo 9:289–297

Wang X, Kang L (2014) Molecular mechanisms of phase change in locusts. Annu Rev Entomol 59:225–244

Wang ET, Kodama G, Baldi P, Moyzis RK (2006) Global landscape of recent inferred Darwinian selection for Homo sapiens. Proc Natl Acad Sci U S A 103(1):135–140

Wanker R, Apcin J, Jennerjahn B, Waibel B (1998) Discrimination of different social companions in spectacled parrotlets (Forpus conspicillatus): evidence for individual vocal recognition. Behav Ecol Sociobiol 43(3):197–202. doi:10.1007/s002650050481

Warburton K, Lees N (1996) Species discrimination in guppies: learned responses to visual cues. Anim Behav 52:371–378

Ward AJW (2012) Social facilitation of exploration in mosquitofish (*Gambusia holbrooki*). Behav Ecol Sociobiol 66:223–230

Ward AJW, Hart PJB (2003) The effects of kin and familiarity on interactions between fish. Fish Fish 4(4):348–358

Ward AJW, Hart PJB (2005) Foraging benefits of shoaling with familiars may be exploited by outsiders. Anim Behav 69(2):329–335. doi:10.1016/j.anbehav.2004.06.005

Ward AJW, Mehner T (2010) Multimodal mixed messages: the use of multiple cues allows greater accuracy in social recognition and predator detection decisions in the mosquitofish, Gambusia holbrooki. Behav Ecolo 21(6):1315–1320. doi:10.1093/beheco/arq152

Ward AJW, Axford S, Krause J (2002a) Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice. Behav Ecolo Sociobiolo 52(3):182–187. doi:10.1007/s00265-002-0505-z

Ward AJW, Hoare DJ, Couzin ID, Broom M, Krause J (2002b) The effects of parasitism and body length on positioning within wild fish shoals. J An Ecolo 71:10–14

Ward AJW, Hart PJB, Krause J (2004a) The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks. Behav Ecolo 15(6):925–929. doi:10.1093/beheco/arh097

Ward AJW, Thomas P, Hart PJB, Krause J (2004b) Correlates of boldness in three-spined sticklebacks (Gasterosteus aculeatus). Behav Ecolo Sociobiolo 55:561–568

Ward AJW, Holbrook RI, Krause J, Hart PJB (2005) Social recognition in sticklebacks: the role of direct experience and habitat cues. Behav Ecolo Sociobiolo 57(6):575–583. doi:10.1007/s00265-004-0901-7

Ward AJW, Duff AJ, Horsfall JS, Currie S (2008a) Scents and scents-ability: pollution disrupts chemical social recognition and shoaling in fish. Proc Royal Soc B Biolo Sci 275:101–105

Ward AJW, Sumpter DJT, Couzin LD, Hart PJB, Krause J (2008b) Quorum decision-making facilitates information transfer in fish shoals. Proc Natl Acad Sci U S A 105:6948–6953

Ward AJW, Webster MM, Magurran AE, Currie S, Krause J (2009) Species and population differences in social recognition between fishes: a role for ecology? Behav Ecolo 20(3):511–516. doi:10.1093/beheco/arp025

Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J (2011) Fast and accurate decisions through collective vigilance in fish shoals. Proc Natl Acad Sci U S A 108:2312–2315

Ward AJW, Herbert-Read JE, Jordan LA, James R, Krause J, Ma Q, Rubenstein DI, Sumpter DJT, Morrell LJ (2013) Initiators, leaders, and recruitment mechanisms in the collective movements of damselfish. Am Nat 181:748–760

Wark AR, Greenwood AK, Taylor EM, Yoshida K, Peichel CL (2011) Heritable differences in schooling behavior among threespine stickleback populations revealed by a novel assay. PLoS One 6(3):e18316

Wark AR, Mills MG, Dang LH, Chan YF, Jones FC, Brady SD, Absher DM, Grimwood J, Schmutz J, Myers RM, Kingsley DM, Peichel CL (2012) Genetic architecture of variation in the lateral line sensory system of three spine sticklebacks. G3 (Bethesda) 2(9):1047–1056

Ward P (1965) Feeding ecology of the black-faced dioch Quelea quelea in Nigeria. Ibis 107(2):173–214

Ward P, Zahavi A (1973) The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis 115(4):517–534

Warner RR (1988) Traditionality of mating-site preferences in a coral reef fish. Nature 335(6192):719–721

Watanabe S, Ito Y (1991) Discrimination of individuals in pigeons. Bird Behav 9(1–2):20–29

Watts DP (2000) Mountain gorilla habitat use strategies and group movement. In: Boinski S, Garber PA (eds) On the move. University of Chicago Press, Chicago, pp 351–374

Way GP, Kiesel AL, Ruhl N, Snekser JL, McRobert SP (2015) Sex differences in a shoaling-boldness behavioral syndrome, but no link with aggression. Behav Pro 113:7–12

Weary DM, Kramer DL (1995) Response of eastern chipmunks to conspecific alarm calls. Anim Behav 49(1):81–93

Webster MM, Hart PJB (2006a) Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. Behav Ecolo 17(6):959–964. doi:10.1093/beheco/arl037

Webster MM, Hart PJ (2006b) Subhabitat selection by foraging threespine stickleback (Gasterosteus aculeatus): previous experience and social conformity. Behav Ecol Sociobiol 60(1):77–86

Webster MM, Laland KN (2012) Social information, conformity and the opportunity costs paid by foraging fish. Behav Ecol Sociobiol 66(5):797–809

Webster MM, Laland KN (2013) Local enhancement via eavesdropping on courtship displays in male guppies, Poecilia reticulata. Anim Behav 86(1):75–83

Webster MM, Laland KN (2015) Space-use and sociability are not related to public-information use in ninespine sticklebacks. Behav Ecol Sociobiol 69(6):895–907

Webster MM, Ward AJW, Hart PJB (2008) Shoal and prey patch choice by co-occurring fishes and prawns: inter-taxa use of socially transmitted cues. Proc Royal Soc B Biolo Sci 275(1631):203–208. doi:10.1098/rspb.2007.1178

Webster MM, Atton N, Hoppitt WJ, Laland KN (2013) Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. Am Nat 181(2):235–244

Webster MS, Hixon MA (2000) Mechanisms and individual consequences of intraspecific competition in a coral-reef fish. Mar Ecol Prog Ser 196:187–194. doi:10.3354/meps196187

Weddle CB, Hunt J, Sakaluk SK (2013) Self-referent phenotype matching and its role in female mate choice in arthropods. Curr Zool 59(2):239–248

Weidinger K, Pavel V (2013) Predator–prey interactions between the South Polar skua Catharacta maccormicki and Antarctic tern Sterna vittata. J Avian Biol 44(1):089–095

Weihs D (1973) Hydromechanics of fish schooling. Nature 241(5387):290–291. doi:10.1038/241290a0

Weimerskirch H, Martin J, Clerquin Y, Alexandre P, Jiraskova S (2001) Energy saving in flight formation – pelicans flying in a 'V' can glide for extended periods using the other birds' air streams. Nature 413(6857):697–698. doi:10.1038/35099670

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size structured populations. Ann Rev Ecolo Syst 15:393–425

Westneat DF, Stewart IR (2003) Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst 34:365–396

Westneat DF, Sherman PW, Morton ML (1990) The ecology and evolution of extra-pair copulations in birds. Curr Ornitholo 7:331–369

Whitehead H (2003) Sperm whales: social evolution in the ocean. University of Chicago Press, Chicago

Whitehead H (2008) Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago

Whitehead H, Waters S, Lyrholm T (1991) Social-organization of female sperm whales and their offspring – constant companions and casual acquaintances. Behav Ecol Sociobiol 29:385–389

Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L (2012) Multilevel societies of female sperm whales (Physeter macrocephalus) in the Atlantic and Pacific: why are they so different? Int J Primatolo 33:1142–1164

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CE, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. Nature 399(6737):682–685

Whitfield DP (1987) Plumage variability, status signaling and individual recognition in avian flocks. Trends Ecol Evol 2(1):13–18

Wiley RH (2013) Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour. Biol Rev 88(1):179–195. doi:10.1111/j.1469-185X.2012.00246.x

Wiley RH, Wiley MS (1977) Recognition of neighbors duets by stripe-backed wrens *Campylorhynchus nuchalis*. Behaviour 62:10–34. doi:10.1163/156853977x00027

Wilkinson GS (1984) Reciprocal food sharing in the vampire bat. Nature 308(5955):181–184

Wilkinson GS, Boughman JW (1998) Social calls coordinate foraging in greater spear-nosed bats. Anim Behav 55:337–350. doi:10.1006/anbe.1997.0557

Williams KS, Simon C (1995) The ecology, behavior, and evolution of periodical cicadas. Annu Rev Entomol 40(1):269–295

Williams KS, Smith KG, Stephen FM (1993) Emergence of 13-yr periodical cicadas (Cicadidae: Magicicada): phenology, mortality, and predators satiation. Ecology 74:1143–1152

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge

Wilson EO (1975) Sociobiology: the new synthesis. Harvard University Press, Cambridge

Wilson EO, Hölldobler B (2005) Eusociality: origin and consequences. Proc Natl Acad Sci U S A 102(38):13367–13371

Wilson ADM, Krause S, James R, Croft DP, Ramnarine IW, Borner KK, Clement RJG, Krause J (2014) Dynamic social networks in guppies (Poecilia reticulata). Behav Ecol Sociobiol 68:915–925

Wingfield JC, Ball GF, Dufty AM, Hegner RE, Ramenofsky M (1987) Testosterone and aggression in birds. Am Sci 75:602–608

Wingfield JC, Hegner RE, Dufty AM, Ball GF (1990) The challenge hypothesis – theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am Natu 136:829–846

Wingfield JC, Lynn SE, Soma KK (2001) Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. Brain Behav Evol 57:239–251

Wisenden BD, Keenleyside MH (1992) Intraspecific brood adoption in convict cichlids: a mutual benefit. Behav Ecol Sociobiol 31(4):263–269

Wittemyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim Behav 69:1357–1371. doi:10.1016/j.anbehav.2004.08.018

Wittemyer G, Okello JBA, Rasmussen HB, Arctander P, Nyakaana S, Douglas-Hamilton I, Siegismund HR (2009) Where sociality and relatedness diverge: the genetic basis for hierarchical social organization in African elephants. Proc Royal Soc B Biolo Sci 276:3513–3521

Wittenberger GF, Hunt JL (1985) The adaptive significance of coloniality in birds. In: Farner DS, King JR, Parkes KC (eds) Avian biology. Academic Press, New York

Wolf NG (1985) Odd fish abandon mixed-species groups when threatened. Behav Ecol Sociobiol 17(1):47–52

Wolf JBW, Mawdsley D, Trillmich F, James R (2007) Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. Anim Behav 74:1293–1302

Wolf M, Kurvers R, Ward AJW, Krause S, Krause J (2013) Accurate decisions in an uncertain world: collective cognition increases true positives while decreasing false positives. Proc Royal Soc B Biol Sci 280:20122777

Woolfenden GE, Fitzpatrick JW (1978) Inheritance of territory in group-breeding birds. Bioscience 28(2):104–108. doi:10.2307/1307423

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75(3):262–300

Wrege PH, Wikelski M, Mandel JT, Rassweiler T, Couzin ID (2005) Antbirds parasitize foraging army ants. Ecology 86(3):555–559. doi:10.1890/04-1133

Wright D, Rimmer LB, Pritchard VL, Butlin RK, Krause J (2003) Inter and intra-population variation in shoaling and boldness in the zebrafish (Danio rerio). J Fish Biol 63(s1):258–259

Wright D, Nakamichi R, Krause J, Butlin RK (2006) QTL analysis of behavioral and morphological differentiation between wild and laboratory zebrafish (Danio rerio). Behav Genet 36(2):271–284

Wrona FJ, Dixon RJ (1991) Group size and predation risk: a field analysis of encounter and dilution effects. Am Nat 137:186–201

Yates CA, Erban R, Escudero C, Couzin ID, Buhl J, Kevrekidis IG, Maini PK, Sumpter DJT (2009) Inherent noise can facilitate coherence in collective swarm motion. Proc Natl Acad Sci U S A 106(14):5464–5469. doi:10.1073/pnas.0811195106

Yen J, Bundock EA (1997) Aggregative behavior in zooplankton: phototactic swarming in 4 developmental stages of Coullana canadensis (Copepoda, Harpacticoida). In: Parrish JK, Hamner WM (eds) Animal groups in three dimensions. How species aggregate. pp 143–162. Cambridge University Press, Cambridge

Yoshimura J, Hayashi T, Tanaka Y, Tainaka KI, Simon C (2009) Selection for prime-number intervals in a numerical model of periodical cicada evolution. Evolution 63(1):288–294

Young KA, Genner MJ, Joyce DA, Haesler MP (2009) Hotshots, hot spots, and female preference: exploring lek formation models with a bower-building cichlid fish. Behav Ecolo 20:609–615

Zahavi A (1977) Testing of a bond. Anim Behav 25(FEB):246–247. doi:10.1016/0003-3472(77)90089-6

Zhang P, Li BG, Qi XG, MacIntosh AJJ, Watanabe K (2012) A proximity-based social network of a group of sichuan snub-nosed monkeys (Rhinopithecus roxellana). Inter J Primatolo 33:1081–1095

Zitterbart DP, Wienecke B, Butler JP, Fabry B (2011) Coordinated movements prevent jamming in an emperor penguin huddle. Plos One 6(6). doi:10.1371/journal.pone.0020260

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DOI 10.1007/978-3-319-28585-6

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