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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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Contents

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

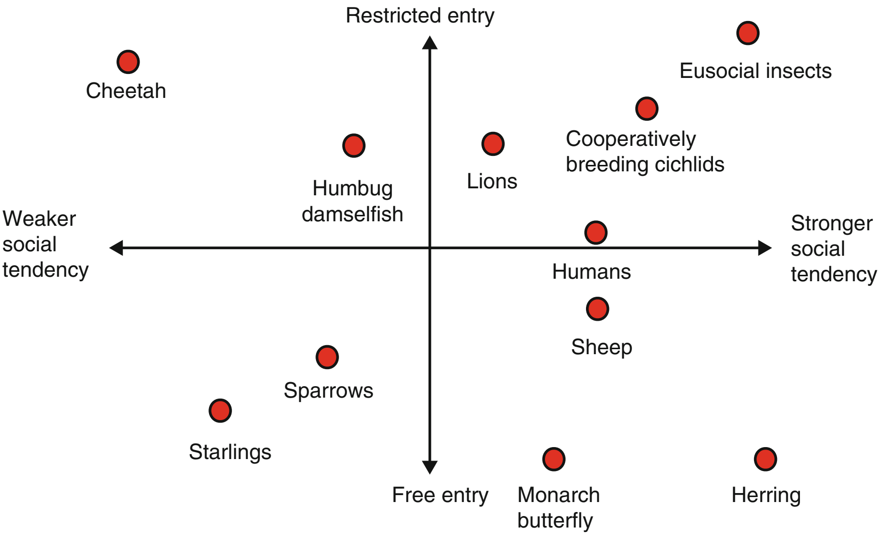

Fig. 1.1 Schematic representation of patterns of sociality among different animal species according to their social tendency and the level of entry restrictions to their group. This initial diagram is qualitative, and the relative positions of species are based on no more than the authors' opinions. 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.

A. Ward, M. Webster, *Sociality: The Behaviour of Group-Living Animals*,
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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