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1 The Evolution of Social Evolution

Dustin R. Rubenstein and Patrick Abbot

Overview

Why do animals live in cooperative groups? How do these societies function? These are the types of questions that motivated both of us in graduate school to study the evolutionary causes and consequences of sociality. We became part of a large and diverse group of scientists studying animal social behavior, a group that today spans the biological sciences, even extending into mathematics, engineering, and more. There are national and international societies, specialized journals, graduate programs, and institutes – each devoted in one way or another to studying animal social behavior. There is a vast body of knowledge about sociality in a diversity of animal species. As we come to know more about social diversity, synthesis has become more challenging. Ambitious, comprehensive narratives in the vein of *Sociobiology* (Wilson, 1975) are all but absent today (Sapp, 1994). But that was not always the case. Early naturalists once composed sweeping treatments of cooperation in nature (Cronin, 1991; Dugatkin, 2006; Dixon, 2008). If you have ever wondered how a wasp is like a bird, with notable exceptions (e.g. Brockmann, 1997; Korb & Heinze, 2008; Székely, *et al*., 2010), you would have to dig deep into the literature to even find them discussed on the same pages. Modern animal behaviorists have become more specialized when it comes to studies of animal societies.

In editing this volume, the two of us were motivated to return to our original graduate school questions, to look beyond the organisms we are familiar with (birds, shrimps, aphids, ants), and begin to synthesize the features of social life that unite disparate animal taxa. In doing so, we take an admittedly optimistic view of animal sociality, arguing that there are convergent and common themes that span vertebrate and invertebrate societies. There is room for debate, and our goal with this book is to re-energize the conversation between scholars who think comparatively about the major animal lineages containing species that form societies.

In this introductory chapter, we begin with a short description of what it means to study sociality and social evolution in animals, and then provide a brief retrospective of studies of animal social behavior from Darwin to the present. We are not historians, and

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our retrospective is incomplete and reflects our own biases. We recommend to the interested reader works such as Crook (1970), Brown (1994), Cronin (1991), Dugatkin (1997, 2006), Costa (2006), Dixon (2008), Gibson, *et al.* (2013) as a start. Instead of a complete history of this field, we emphasize some of the key empirical and theoretical insights that led to advances in the study of social evolution, as well as some of the scientists responsible for these discoveries. We further discuss those researchers whose theories, empirical studies, or published volumes have attempted to bridge the divide between social vertebrates and invertebrates. We then highlight previous attempts to synthesize animal sociality, and discuss the structure of the chapters in this book as a way to begin analyzing these ideas in a new way. We lay out a “bottom-up” approach to dissecting animal societies, first by summarizing the distinct terminologies that researchers studying sociality use to describe the different forms of animal societies, then by discussing the various reasons that groups form and the numerous factors that influence their formation. Finally, we discuss the types of life history traits that are important for characterizing both social species and the groups that they form. Ultimately, this chapter is but a starting point for the book, which is itself a call for a renewed focus upon an empirical and theoretical unification of animal social life.

1.1 Sociality and the Definition of Animal Societies

What is sociality? This is not an obvious question. After all, nearly all animals are social at some point during their lives: individuals often exhibit affiliative or aggressive social interactions with members of their own species, and individuals in nearly all species must come together to mate (Trivers, 1985; Kokko, 2007). Many species also form groups, either ephemerally or permanently, including colonies of nesting seabirds, herds of migrating ungulates, schools of swimming fish, aggregations of feeding insects, or assemblages of mating amphibians (Alexander, 1974; Krause & Ruxton, 2002). The most advanced groups – eusocial insect societies – are described by three criteria first introduced by Batra (1966) and later expanded by Michener (1969) and Wilson (1971): (1) overlapping generations; (2) cooperative care of young; and (3) reproductive division of labor (i.e. many individuals in a group are temporarily or permanently sterile). Although originally created to define eusocial societies in insects, these criteria have also been used to describe cooperatively breeding societies in vertebrates (Sherman, *et al.*, 1995), as well as the societies of other invertebrates like aphids and thrips (Chapter 6), spiders (Chapter 7), and shrimps (Chapter 8). Most of these societies consist of kin (i.e. they are family groups), though this is also not a prerequisite for cooperative societies (Riehl, 2013). For many researchers, social groups consist of individuals who cooperate, but for others, cooperation is not a defining characteristic. What then are the characteristics of animal societies, and how should sociality be defined?

It turns out that researchers have a difficult time defining the term sociality, as it means different things in different fields. We define sociality for the purposes of this book simply as cooperative group living. This intentionally broad definition encompasses species that have at least some form of reproductive division of labor, and thus is similar to the broad approach taken by others in their treatments of species that grade from simple to complex social living (e.g. Korb & Heinze, 2008; Bourke, 2011). However, we also asked our authors to consider species that form non-ephemeral groups lacking reproductive division of labor. Moreover, we asked that they consider species that exhibit kin structure (i.e. form family groups), but also those that do not live with kin. Our definition also describes species where some group members cooperatively care for young that are not their own (i.e. alloparental care), but others where there is no communal care of offspring. Thus, our definition of sociality by necessity encompasses a range of forms of social organization. While we may have erred on the side of being too broad, the key element these species share is that some form stable groups within which various cooperative behaviors are typically expressed.

While this definition will not entirely satisfy all of the readers – or even all of the authors – it is a starting point from which we can begin to explore the similarities and differences among animals that are often described as being social. Indeed, one of the primary goals of this book is to detail the diversity of social lives that animals exhibit. It is therefore not surprising that the scientists who study social animals define sociality a bit differently. Sociality as we define it here occurs in less than 2 percent of insects (eusociality), and in only about 5 percent of mammals and 9 percent of birds (cooperative breeding) (Wilson, 1971; Cockburn, 2006; Lukas & Clutton-Brock, 2012). Sociality is even rarer among fishes, shrimps, lizards, spiders, and most of other taxonomic groups covered in this book. But while sociality is rare, what is obvious is that there are common features to social life in animals. The same patterns show up repeatedly in disparate animal lineages. The unique features of different animal groups help to explain why empirical studies of social vertebrates and invertebrates have largely taken divergent, though often parallel, paths over the last century.

1.2 The Importance of Studying Sociality

Why should you care about sociality? Whether or not you think ants or meerkats are fascinating, how convincing you find any argument for studying animal social behavior may depend upon your perspective. Even if you like to avoid bees or wasps, you may be persuaded by that fact that social insects probably account for about half of all of the biomass of the planet's biological diversity, and that ants and termites dominate the terrestrial habitats in which they occur (Wilson, 1990; Hölldobler & Wilson, 1990; Wilson, 2012) or that an unmistakable pattern in the evolution of all life on earth is that transitions in levels of organization have repeatedly occurred, in which formerly independent units (e.g. genes, chromosomes, cells, individuals, and so on) bind their fates together in a social enterprise, overcoming freeloaders (i.e. individuals who reap the benefit but pay no cost) in the process (Maynard Smith & Szathmáry, 1995; Queller & Strassman, 2009; Bourke, 2011). Or maybe you would be convinced by arguments closer to home: how, for example, studying sociality informs our understanding of ourselves (Pinker, 2010) and the development of our own societies (Fukuyama, 2011). Ultimately, the goal of those studying sociality and social evolution is to account for the special nature of social organisms (Strassmann & Queller, 2007), and to the extent that all organisms are, one way or another, social, the study of sociality is not only integral to the study of biology, but to all life on earth.

1.3 A History of Taxonomic Divergence

William D. Hamilton's (1936–2000) publications in 1964 on kin selection (Hamilton, 1964a,b), followed by the publication of Edward O. Wilson's *Sociobiology* in 1975, mark the start of what many would recognize as the beginning of the modern study of social behavior (Dugatkin, 1997; Costa, 2006; Clutton-Brock, *et al.* 2009). However, comparative approaches to social behavior have their origins almost a century earlier in the years following *On the Origin of Species* (Darwin, 1859), in the emerging fields of sociology and ecology (Crook, 1970). As many scholars have noted, Charles Darwin (1809–1882) was not a neo-Darwinian (Cronin, 1991; Browne, 2002; Dixon, 2008), particularly when it came to social behavior. Altruism was a word that neither he nor most of his contemporaries used (Dixon, 2008). Yet, in the decades that followed the publication of *On the Origin of Species* (Darwin, 1859), studies of animal social behavior proliferated, as moral philosophers, natural historians, political economists, theologians, and nascent sociologists turned to nature to discover the biological roots of moral philosophies, or to gauge the merit of positivist theories of human social development and progress. Their interests were largely philosophical and political, and only later did they become zoological. Was social behavior red in tooth and claw, as the prevailing interpretation of Darwin held in the late nineteenth century? Or was social life a regular, even progressive, outcome of natural laws?

In both Europe and America, the two decades that immediately followed the publication of *On the Origin of Species* were characterized by economic and social upheaval. Rapid changes in industrialization were accompanied by efforts to realign political, economic, and social orders. Darwin's book was a bestseller, but it was not uncommon for his theories on natural selection to be misunderstood, ignored, or even ridiculed; a "law of higgledy-piggledy," as Herschel famously put it (Browne, 2006; Hull, 2011). Even before the publication of *On the Origin of Species,* philosophers and political theorists turned to the natural world for both definition, validation, and critiques of Victorian society (Clark, 2009). A growing middle class, industrialization, urbanization, secularization, and a social reform movement were among the drivers of a growing fascination with the lessons and curiosities of animal life. Herbert Spencer (1820–1903) coined the phrase "survival of the fittest," and advocated for the natural progression of societies from simple to more complex via a mixture of Darwinian and Lamarkian reasoning. Spencer is largely forgotten today, but he was enormously influential, because he inspired a generation of devotees who melded sociological inquiry with avid study of animal social life (Francis & Taylor, 2015). One such devotee was Alfred Espinas (1844–1922), a French doctoral student who took a great interest in animal social behavior and in 1877, published *On Animal Societies* (Espinas, 1877), which summarized the existing knowledge of animal sociality at the time. His goal was to justify the Spencerian vision of an organic progression of society based upon natural laws, rather than moral imperatives (Brooks, 1998). Espinas' book, like those of other nascent sociologists, influenced a number of early biologists working on social behavior in the early and mid-twentieth century. Similarly, the Russian, Petr Kropotkin, published *Mutual Aid: A Factor in Evolution* in 1902 (Kropotkin, 1902), which posited a universally cooperative principle organizing the natural world, in opposition to the struggle for existence that was the prevailing, though incorrect, synopsis of Darwin's thesis. Other important texts from this era included *Animal Life: A First-Book of Zoology,* first published in 1900 by David Jordan (1851–1931) and Vernon Kellogg (1867–1937), which provided a broad synopsis of animal ecology, including mutualistic and social interactions in animals, and Benjamin Kidd's (1858–1916) bestseller *Social Evolution*, an ultimately discredited volume published in 1894 that popularized evolutionary ethics and became associated with social Darwinist movements (Crook, 1980).

Enthusiasm waxed and waned in the early decades of the twentieth century for the positivist ideals and naturalistic moralisms of the French philosopher Auguste Comte (1798–1857) and the late Victorians, preempted by the emergence of reductionism and the "fissioning" of the life sciences (Sapp, 1994). The result was, as Crook (1970) notes, a considerable gap in the social behavior literature in the period before World War II. Yet, holism gathered momentum both in Europe and America, at places like the University of Chicago and other campuses and field stations (Gibson, 2012). William Morton Wheeler (1865–1937) was an American entomologist who, having already published extensively on ants and other insects for nearly two decades, formulated views of ant and termite societies as more than the sum of their parts, as superorganisms (Wheeler, 1911; 1928). Since the Greeks, social insects had been used as mirrors of human societies (Costa, 2002). Victorian naturalists and political economists found in ants and bees validations of social order and the merits of division of labor (Clark, 2009). Wheeler, influenced by Weismann's cell theories, made remarkable descriptions of the organizations of ant societies that fueled the first elaborations of what we now recognize as the levels of selection (Gibson, 2012; Gibson, *et al.* 2013).

Meanwhile, Julian Huxley (1887–1975) was laying the foundations for the new field of ethology with his studies of courting behavior in grebes and other birds (Huxley, 1914; Brooke, 2014). The ethological tradition, fostered by Huxley and fellow ornithologists Niko Tinbergen (1907–1988), Konrad Lorenz (1903–1989), and David Lack (1910–1973), posited a comparative and experimental approach to animal behavior built upon both mechanistic and evolutionary principles (Brown, 1994; Burkhardt, 2014), and most importantly, close observation. This was the milieu out of which Alexander Skutch (1904–2004) made the first detailed observations of the family lives of neotropical birds (Stiles, 2005). Skutch, a polymath, naturalist, and leading ornithologist, published *Helpers at the Nest* in 1935, which included the first systematic observations in birds of cooperative care of young by non-breeding auxiliaries who aid in raising others' offspring (i.e. helpers). Skutch's descriptions of cooperative breeding behavior in three species of Central American birds (Skutch, 1935), followed by his much broader accounts a few decades later (Skutch, 1961), inspired later generations of scientists to study vertebrate social behavior, and although largely ignored for decades, marked the origin of thinking about cooperative breeding in vertebrates as an evolutionary and ecological problem (Brown, 1978).

Wheeler and Skutch were both expert naturalists whose traditions of fieldwork helped the study of social behavior re-emerge after World War II. Wheeler died in 1937, and though he mentored many students, many moved on to other fields, such as Alfred Kinsey of "human sexology" fame. Thus, despite the work of ethologists and entomologists like Wheeler on ants and Karl von Frisch (1886–1982) on bees, the roots of a taxonomic schism emerged in the study of social evolution. Animal behavior was founded as a discipline by ornithologists, while social insect biologists devoted their attention to taxonomy, morphology, and especially physiology. The focus on mechanisms accompanied the rejection of holism and "emergent evolution" by scientists newly minted in atomic age reductionism (Gibson, *et al.*, 2013). In essence, there were not many entomologists at the table at the time when studies of social behavior and comparative evolutionary biology were beginning to blossom. Warder Allee (1885–1955) stands out during this period as the inheritor of a tradition for comparative studies of social evolution, for which he received only modest recognition for most of his career (Mitman, 1992; Dugatkin, 2006). His focus, however, was centered upon developing Kropotkin-like universals about the overarching role of cooperation in nature, and many of his works, couched in the language of demography and the nascent field of ecology, had little influence on his contemporaries until late in his life.

This taxonomic schism during the postwar years was exemplified in the difficulties that a young Hamilton had in convincing his graduate mentors in the early 1960s that there were indeed interesting evolutionary problems posed by altruism in ants and bees (Segerstrale, 2013). However, Hamilton eventually not only succeeded in convincing his mentors that individually costly, but helpful, behaviors were worth thinking about, but he changed forever how we study social behavior. As Brown (1994) pointed out, Hamilton's theoretical advances on the genetics and evolution of altruism, with insects in mind, came at a time when Lack and other ornithologists were developing an empirically informed ecological framework for comparing different social systems in birds. At the same time, Crook and Gartlan (1966) were establishing ecological comparative studies of primates and other mammals. Thus, by 1970, the ingredients were in place for the emergence of a socioecological framework for comparative social behavior and evolution. And yet, empirical studies of social insects and cooperatively breeding birds and mammals proceeded largely independently, despite the emergence of this new unifying theory of inclusive fitness. Empirical insights from testing Hamilton's theory would arrive piecemeal from an early fission into vertebrate and invertebrate camps that Wilson (1971), building upon a tradition inherited from the likes of Crook and Allee (Allee, *et al.*, 1949), would bridge.

1.4 Attempts at Social Synthesis

Inclusive fitness theory is an explicit framework that governs the evolution of social traits, irrespective of taxonomy (Hamilton, 1964a,b; Bourke, 2011). The broad utility of

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Hamilton's rule – and inclusive fitness theory more generally – is born out in its simplicity. According to Hamilton's Rule, a social action will be favored when its positive effect on indirect fitness is greater than its direct fitness cost. In simple math, rb more than c, or the product of the relatedness (r) between two individuals and the fitness benefit (b) an individual receives from the action valued against the fitness cost (c) to the individual expressing the action. Hamilton's concept – termed kin selection by Maynard Smith (1964) – was the foundation for Wilson's *Sociobiology*, as well as many of the later theoretical contributions to the field. Most of these subsequent theoretical contributions were synthetic in their nature, generating hypotheses that were later tested in organisms as diverse as birds, wasps, and microbes (e.g. Eberhard, 1972; Emlen & Wrege, 1988; Griffin, *et al.* 2004). The theoretical contributions of Trivers (1971, 1974) and others on cooperation and conflict also apply equally well across all taxonomic groups, and ultimately shaped the thinking of many empiricists. The development of reproductive skew theory (Vehrencamp, 1977), an extension of Hamilton's rule, has also been tested empirically in birds, mammals, and numerous species of insects (Keller & Reeve, 1994; Hager & Jones, 2009). The generality of these theories, the alluring examples of convergence across disparate taxa, and a Darwinian/Spencerian tradition of unification and comparative approaches spurred a number of researchers to generate broadly synthetic summaries of social life. For example, Alexander (1974) discussed forms of social behavior (kin-selected or otherwise) in very general terms, largely avoiding specific taxonomic language in much of his review. Trivers (1985) and Bourke (2011) discussed aspects of social evolution common to all animal societies. Andersson (1984) and later Brockmann (1997) recognized the similarities between cooperatively breeding birds and eusocial insects. Sherman, *et al.* (1995) argued that species from different taxonomic groups could be arrayed along a continuum of reproductive sharing, or reproductive skew, though this synthetic idea was criticized by those who saw eusociality as something unique to insects and were reluctant to recognize potential parallels between insects and vertebrates (e.g. Crespi & Yanega, 1995; Costa & Fitzgerald, 1996a,b; Wcislo, 1997a,b; Costa & Fitzgerald, 2005; Crespi, 2005; Wcislo, 2005). Other researchers have suggested alternative views on how disparate social taxa could be linked (Aviles & Harwood, 2012), and some have extended what we know about cooperation in animals to human societies (e.g. Crespi, 2013). Edited volumes by Rubenstein and Wrangham (1986) and later Choe and Crespi (1997) explored social evolution in vertebrates (birds and mammals) and invertebrates (insects and arachnids), respectively, as did the book *The Other Insect Societies*, by Costa (2006). In addition to these treatments comparing social behavior within animal lineages, edited volumes by Slobodchikoff (1988) and Korb and Heinze (2008) began to explore the similarities and differences in social vertebrates and invertebrates, largely from an ecological perspective.

In summary, the very earliest studies of social behavior were comparative, but they were conducted by moral philosophers, natural historians, political economists, theologians, and nascent sociologists, not by biologists. It was the early decades of the twentieth century, when academic departments were constructed around taxonomy and natural history, that entomological and vertebrate research agendas initially diverged. It was not until the theoretical advances of the mid-century that the first attempts at a modern social synthesis began. These mathematical models applied equally well to all social organisms – invertebrates, vertebrates, or even microbes. However, to a large extent, the breadth of social evolutionary theory has not been matched by equally broad empirical research programs. Given the wealth of new comparative methods for analyzing large datasets of life history traits and biogeographic data, as well as the explosion and growing affordability of comparative genomic tools, the time is right to reconsider a social synthesis, from both a theoretical and empirical perspective. This book is an attempt to do just that: to comparatively survey the diversity of vertebrate and invertebrate societies, and lay the groundwork for a new generation of theoretical, empirical, and comparative studies of animal social evolution.

1.5 Comparative Social Evolution: Social Diversity, Traits and Synthesis

The goal of this book is to synthesize the features of animal social life across the principle taxonomic groups in which sociality has evolved, and do so in a cohesive and comparative manner by centralizing the review within a single volume and with a unified format. Our book differs from previous treatments in that it takes a “bottom-up” rather than a “top-down” approach to explore social evolution. That is, instead of emphasizing the theoretical advances that seemingly link disparate taxa (e.g. kin selection) or a consideration of shared evolutionary histories (e.g. the Hymenoptera), the bulk of each chapter on a given taxonomic group instead discusses the traits and characteristics of social (and non-social) species and the groups that they form. Our intent is to highlight much of the interesting natural and life history data that attracted us and other scientists to study social organisms in the first place. Identifying a suite of traits shared among social species and groups may ultimately allow researchers to better define the social phenotype, and then study the proximate and ultimate factors that shape its evolution. Ultimately, each chapter is comparable in both structure and content, so scholars of one type of organism can readily compare and contrast with those from other taxonomic groups.

To achieve our bottom-up approach to exploring social evolution, each chapter in the book is structured similarly. Using a uniform chapter structure was challenging, since some sections apply to some taxa better than they do to others. Yet, exploring the same life history traits, ecological factors, and other characteristics of social species and groups across all taxonomic groups provides opportunities to observe previously unrecognized patterns. The chapters themselves are grouped into three parts. Part I briefly explores the social diversity within a taxonomic group, highlighting the frequency, forms, and reasons that social groups develop, as well as the evolutionary and ecological factors that shape social living. Part II describes the social phenotype in greater detail, highlighting both the traits of social species and of the social groups that they form. Finally, Part III begins to synthesize social diversity, both within a taxonomic group, as well as among groups and across lineages. Next, we describe briefly

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why chapters are structured the way that they are, and how doing so can begin to shed light upon the comparative social evolution of such disparate organisms.

1.5.1 Social Diversity

Both the frequency of occurrence and diversity of form of animal societies vary greatly within and among taxonomic groups. Sociality is ubiquitous in groups like the ants where all of the more than 15,000 species are eusocial (Chapter 2), but it is extremely rare, for example, in spiders (Chapter 7), shrimps (Chapter 8), and freshwater fishes (Chapter 12). Animal societies also vary widely in form, and we know that the most well-studied species often do not exhibit the most common form of society. For example, it can be a common assumption that most bees are like honeybees and live in eusocial societies with a single queen and hundreds of workers, but in fact, most bee species are solitary or live in small groups consisting of several adult females (Chapter 3). Additionally, within cooperatively breeding birds, most species live in family groups with helpers, though some family-living species lack helpers and some species form social groups of unrelated individuals (Chapter 11).

A synthetic discussion about the variation in form and structure of animal societies is often difficult because the criteria and terminology that researchers use to describe animal societies varies among taxonomic groups. In addition to the jargon that uniquely describes specific taxonomic groups (see the glossary), at even the broadest scale, the terms that describe basic reproductive structures in vertebrates and invertebrates differ greatly (Rubenstein, *et al*., 2016). For example, vertebrate societies are often divided into those with a single breeding pair (singular breeding) and those with more than one breeding pair (plural breeding) (Brown, 1987; Solomon & French, 1997). Although the same categorization is often used to describe eusocial insect societies, the terminology used by entomologists is very different. Invertebrate societies with a single queen are typically referred to as being monogynous, whereas those with multiple queens are referred to as polygynous. Sometimes, the multi-queen/multi-breeder societies are called communal in both invertebrate and vertebrates, but even in cooperatively breeding birds and mammals, communal breeding is used to describe different behaviors (Chapter 14). In other words, the lineage-specific terminology used to categorize the most basic social structures, as well as the taxon-specific jargon that describes the forms of animal societies, often hinders our ability to compare and contrast disparate social animal groups. Taking a bottom-up approach to describe the demographic and breeding structures of groups may ultimately help alleviate some of this terminological confusion by quantifying societies continuously rather than categorically.

Despite the terminological differences in how animal societies are described and defined, there are many similarities across taxonomic groups in why societies form. At the most basic level, animal societies often form because the benefits (either direct or indirect) of grouping outweigh the costs of breeding independently (Hamilton, 1964a,b; Bourke, 2011). The relative importance of direct versus indirect benefits has been debated in the literature (e.g. Clutton-Brock, 2002). While there are a variety of potential direct benefits individuals receive by living in groups (Krause & Ruxton,

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2002), individuals most often group to gain access to resources and avoid predators (Alexander, 1974), and in some species, to maintain homeostasis, to gain access to mates, or to provide offspring care. Although not all organisms achieve all of these benefits, it is often surprising to learn which species reap which rewards. For example, the benefits of homeostasis obviously apply to many eusocial insects that maintain a constant temperature inside the nest, but homeostatic benefits are also important to a number of avian species (Chapter 11), cavity-nesting primates (Chapter 9), denning mammals (Chapter 10), and even some lizards (Chapter 13).

Ecological factors have long been thought to play a key role in shaping social behavior and mating systems in vertebrates and insects (Alexander, 1974; Jarman, 1974; Emlen & Oring, 1977; Bourke & Heinze, 1994). Ecology can constrain the formation of groups by limiting dispersal and independent breeding (Emlen, 1982), as well as influence the biogeographic distribution and niches of social groups and species (Jetz & Rubenstein, 2011). Climate – considered to be part of ecology – can also influence the broad-scale distribution of social species in vertebrates (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011) and invertebrates (Kocher, *et al.*, 2014; Purcell, *et al.*, 2015; Sheehan, *et al.*, 2015). Indeed, climate, ecology, and biogeography often interact to influence the evolution and distribution of social species. For example, the high incidence of cooperative breeding in Australian birds is the product of both the continent's variable and semi-arid environment (Jetz & Rubenstein, 2011), as well the biogeographic and evolutionary history of its avifauna (Cockburn, 1996; Cockburn 2013; Chapter 11).

Finally, evolutionary history also plays an important role in explaining the distribution of social species within a taxonomic group. For example, within the Hymenoptera (ants, bees, and wasps), the evolutionary histories of social clades vary among orders. Eusociality has evolved independently and repeatedly in numerous clades of bees (Chapter 3) and wasps (Chapter 4), but only once in ants (Chapter 2). However, in groups like the birds (Chapter 11), cooperative breeding evolved early in the radiation, but has since been lost and regained many times across the avian tree of life (Ligon & Burt, 2004; Chapter 11). Moreover, life history constraints resulting from shared evolutionary history often combine with ecology to influence the evolution of sociality in birds (Arnold & Owens, 1998; Hatchwell & Komdeur, 2000).

1.5.2 Social Traits

A discussion of the potential direct benefits, costs, and evolutionary constraints on social grouping is arguably a top-down approach that summarizes what we already know – or think we know – about social diversity within a given group of animals. In contrast, taking a bottom-up approach that searches for the similarities and differences in animal societies across disparate animal lineages requires a systematic summary of the traits that characterize both social species and the groups that they form. However, choosing which traits to summarize is not an easy task. The most thoroughly studied life history traits of social species for comparative studies represent different components of the breeding life histories of social animals – lifespan and longevity, fecundity, age at

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first reproduction, dispersal, and so on. We also consider cognition and communication, traits that define many social species (e.g. brain size) and that allow societies to function efficiently and effectively. After all, most social organisms require mechanisms to recognize group mates, identify individuals or kin, and then coordinate their actions (Hauber & Sherman, 2001). Finally, when considering the life histories of social species, it is important to do so within the broader context of non-social species, particularly within taxonomic groups where sociality is rare. Thus, wherever possible, we asked the authors to frame the life histories of social species in the context of closely related non-social species.

Although many of the life history traits of social species have been quantified in a variety of taxonomic groups, it turns out that they are not always comparable. That is, specific life history traits often mean different things in different lineages and are sometimes quantified in very different ways. For example, longevity in vertebrates is typically measured in terms of individual lifespan (median or maximum), but many social insects are measured in terms of colony or queen lifespan (maximum).

Defining the traits of social groups is also not easy. Doing so is complicated by the fact that the terminology researchers use to define animal societies varies immensely across taxonomic groups. For example, primate and other mammalian societies are often defined by three components: (1) social organization; (2) mating system; and (3) social structure (Kappeler & van Schaik, 2002; see also Chapters 9 and 10). Within this framework, social organization refers to who lives with whom, mating system refers to who mates with whom, and social structure refers to the social relationships among group members. However, these same terms are often defined very differently in other taxonomic groups, even in the following chapters. In our bottom-up approach to editing this book, we chose not to force a single terminology onto the authors of each chapter. Instead, we begin to highlight some of these terminological differences here, and then return to this point at the book's conclusion (Chapter 14).

We believe that separating social and mating interactions and bonds – as Kappeler & van Schaik (2002) did – needs to be one of the primary goals of any definition of animal sociality. Most animal behaviorists recognize the clear distinction between the social system (e.g. cooperative breeding, eusociality, etc.) and the mating system (e.g. monogamy, polygyny, polyandry, polygynandry). After all, within a given type of social system, a variety of mating systems can occur (e.g. different cooperatively breeding bird species can be monogamous, polygynous, polyandrous, or polygynandrous [Cockburn, 2004]; or within and among ant species, queens can be either monogamous or polyandrous [Keller, 1993]). Additionally, researchers often emphasize the role of genetic relatedness in the study of social evolution, a tradition that derives from Hamilton's (1964a, b) seminal work. Genetic structure, often referred to as kin structure, within a group is greatly influenced by the mating decisions of female breeders (Boomsma 2007, 2009, 2013). Lifetime monogamy by females results in high relatedness among offspring, which is thought to influence the evolution of eusociality in insects (Hughes, *et al.*, 2008) and cooperative breeding in birds (Cornwallis, *et al.*, 2010) and mammals (Lukas & Clutton-Brock, 2012). However, kin structure within a social group is also influenced by the number of females that breed in a group (Rubenstein, 2012; Boomsma,

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et al., 2014). Indeed, in some insects, there is a trade-off between the number of queens in a colony and the number of mates each queen has (Kronauer & Boomsma, 2007). Thus, it is important to keep the concepts of social structure and mating system separate when defining animal societies because the genetic structure of social groups can be influenced by both the number of mates a breeding female has (the mating system), as well as the number of breeding females in the group (the social structure).

To keep these two ideas – social structure and mating system – apart, there is a section in each chapter devoted to each concept. We first explore the variation in genetic structures within societies of each taxonomic group. Although some taxonomic groups are much better studied than others, we explore not only the genetic structure of societies, but also their mating patterns and systems. Following this, our exploration of the social structure focuses upon the demographic structures of groups (e.g. group structure, breeding structure, and the sex ratio). This includes discussion of the variation in the number of breeders/reproductive versus helpers/workers in animal societies, as well as the different sex ratios within and among these social categories. Ultimately, categorizing the variation in demographic and breeding structure is, easier for some groups than others: shrimps (Chapter 8) are easier than ants (Chapter 2), for example, because the former have an order of magnitude fewer social species than do the latter. Nonetheless, it remains important to consider the variation in demographic and breeding structure of animal societies for any comparative approach.

1.5.3 Social Synthesis

By exploring both the traits that define the phenotype of social organisms as well as those that describe the form and structure of the groups that they form, we can begin to synthesize the diversity of social life within and across taxonomic groups. The final section of each chapter is devoted to doing exactly this. Authors were given more leeway here to explore patterns of social life within their taxonomic group, as well as to begin to make links to other groups within this book. Ultimately, the goal of this section is for readers to start to synthesize the material in each chapter and begin to make further connections between disparate animal groups. We then continue and expand upon these syntheses at the end of the book in the concluding chapter (Chapter 14).

1.6 The Prospect of Social Convergence

Theory has always been a critical component of the field of animal social behavior, often working hand-in-hand with empirical studies. As we discussed earlier, Hamilton's theory of kin selection (Hamilton, 1964a,b) not only set the stage for a generation of empirical studies, but those same empirical studies helped refine our theoretical predictions. For example, the discovery of diploid eusocial naked mole-rats (Jarvis, 1991), coupled with the appreciation of diploidy in eusocial termites, helped to reframe kin selection as something more than a synonym for haplodiploidy. Reproductive skew theory (Vehrencamp, 1977) extended Hamilton's rule and led empiricists to focus upon

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two of its key components, the roles that genetic relatedness and ecological constraints play in shaping the formation of groups and altruistic behaviors. Arguably, insect biologists have emphasized the genetic relatedness in their studies of social evolution, whereas vertebrate biologists have emphasized ecological constraints (Elgar, 2015). Yet more recently, entomologists have begun to consider the role that ecology plays in shaping eusocial insect societies (e.g. Kocher, *et al*., 2014; Purcell, *et al*., 2015; Sheehan, *et al*., 2015), and vertebrate biologists have begun to study the role of genetic relatedness in driving the evolution of cooperative breeding behavior independently from any ecological factors (e.g. Cornwallis, *et al*., 2010; Lukas & Clutton-Brock, 2012).

Although cross-fertilization is occurring between biologists who study invertebrate or vertebrate sociality, the two sub-fields remain largely distinct. Can we ultimately achieve the social synthesis that kin selection and reproductive skew theory promised decades ago? We remain optimistic that not only can a unified theory of sociality be developed, but that empirical studies of social animals can become more integrated across taxonomic boundaries. This book is a first attempt to do this by beginning to compile relevant concepts and summarize key social traits across all animals. We return to this goal at the end of the book (Chapter 14) and discuss what can be learned from thinking about sociality in different taxonomic groups in the same way.

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