14 Social Synthesis

Opportunities for Comparative Social Evolution

Dustin R. Rubenstein and Patrick Abbot

Overview

As we have learned throughout the chapters of this book, sociality – defined broadly as cooperative group living (Chapter 1) – occurs in diverse animal species. Through consideration of the traits of these social species, as well as those of the groups that they form, some broad-scale similarities and differences start to emerge. Here we begin to explore some of the ways that life history shapes – or is shaped by – sociality, by summarizing the traits of social species and social groups. We use Hamilton's rule to guide our analysis, and note as others have, that one challenge to synthesis has been the degree to which invertebrate and vertebrate biologists have emphasized different parameters of this equation (Elgar, 2015). We argue that traits of the social group should be used to describe social organization, and that traits of social species be used to describe social syndromes. We then introduce a simple categorization scheme that uses just four key social traits of the group, and emphasize two emergent social syndromes. We highlight a number of areas ripe for trait-based comparative work, particularly in an age of genomics. Just as this book is meant to be a starting point for dialogue about comparative perspectives on the evolution of sociality, so too is this chapter meant to be a first attempt at using life history data from the diversity of animal taxa containing social species to generate new social synthesis, ideas, hypotheses, and research agendas. A trait-based approach is particularly important as we enter the genomic era because it will help guide a true comparative evolutionary approach for studying sociality, especially if we apply a systems approach.

We acknowledge all of the authors who wrote chapters for this book for their hard work and dedicated study of social animals. Their thorough and insightful descriptions of social animals set the stage for not only this chapter, but for future attempts at social synthesis. We also thank the many taxonomic specialists who helped review the chapters. Dustin Rubenstein (IOS-1121435, IOS-1257530, IOS-1439985) and Patrick Abbot (IOS-1147033) were both supported by the US National Science Foundation, and thank Michelle Elekonich for her assistance. We also acknowledge the National Evolutionary Synthesis Center (NESCent), which supported many of the authors. We thank Judith Korb, Eileen Lacey, and Dan Rubenstein for constructive comments on previous versions of this chapter. We thank Brandi Cannon and Ian Hewitt for helping to copy-edit not only this chapter, but all of the chapters in the book.

14.1 Patterns of Social Diversity

The honeybee is one of the most recognizable of social organisms. Within a colony, a single queen can produce up to tens of thousands of worker bees that divide tasks and cooperatively coexist. Yet, as we learned in Chapter 3, most bees are not social; the majority of bees are solitary creatures. In contrast to the bees are the ants, a group closely related to bees in which, as we learned in Chapter 2, all of the more than 15,000 species are eusocial. Similarly, the nearly 3000 species of termites (Chapter 5) are also all eusocial. In most taxonomic groups, however, social species occur only in a subset of lineages. For example, in shrimps (Chapter 8) and freshwater fishes (Chapter 12), all of the known social species occur within a single genus. In wasps (Chapter 4), another close relative of the bees, sociality occurs in only in 3 of 37 families, and in spiders (Chapter 7), only a few dozen of the nearly 50,000 described species are social. Indeed, sociality occurs in less than 2 percent of all insects, and in only about 5 percent of mammals and 9 percent of birds (Wilson, 1971; Cockburn, 2006; Lukas & Clutton-Brock, 2012).

If sociality is so rare, why is studying its evolution so important? As we highlighted in Chapter 1, an obvious reason is the fact that we are social, as are many of the most charismatic megafauna on earth. But social species are often ecologically and evolutionarily important. Ants and termites dominate the terrestrial habitats in which they occur, and account for about half of all of the biomass of the planet's biological diversity (Wilson, 1990; Hölldobler & Wilson, 1990; Wilson, 2012). Many of the eusocial insects also exemplify one of the major evolutionary transitions in life, as individuals cooperate and coordinate their behavior to from a collective, "superorganism" in some of the most extreme cases (Maynard Smith & Szathmáry, 1995; Hölldobler & Wilson, 2008; Queller & Strassman, 2009; Bourke, 2011). As has been pointed out by others, there are few traits that do not affect social interactions one way or another (Szèkely, *et al.*, 2010). The study of sociality is therefore not only integral to the study of biology, but to all life on earth.

To any casual observer, it would seem that sociality has been well studied over the past century. However, one point that many of the chapters in this book have made clear is that not all social species have been given equal attention. There has been a greater focus on the Hymenoptera (ants, bees, and wasps) than on any other group of social organisms (Elgar, 2015). Many of the authors in this book make an explicit call for greater work on some of the least studied organisms. For example, Hultgren, *et al.* (Chapter 8) and Taborsky & Wong (Chapter 12) argue that sociality in marine species is much less studied than in terrestrial or freshwater species. In the vertebrates, social lizards (Chapter 13) are much more poorly studied than cooperatively breeding mammals (Chapter 10) or birds (Chapter 11). Even within the Hymenoptera, it is remarkable how much diversity remains unexplored. Clearly, there is a need for comparative perspectives on animal social evolution that embrace the full diversity of social animals (see previous treatments in Rubenstein & Wrangham, 1986; Choe & Crespi, 1997; Korb & Heinze, 2008a). The "bottom-up" approach that we advocated for in Chapter 1 (i.e. using a trait-based approach to identify similarities and differences in the traits of social species and the groups that they form, rather than a “top-down” approach that prescribes a theoretical framework based upon the hypothesized reason that groups form) can help inform us about what to study in each of these species. The data compiled here should illuminate which areas and types of life history traits need greater attention, even in the best-studied social species.

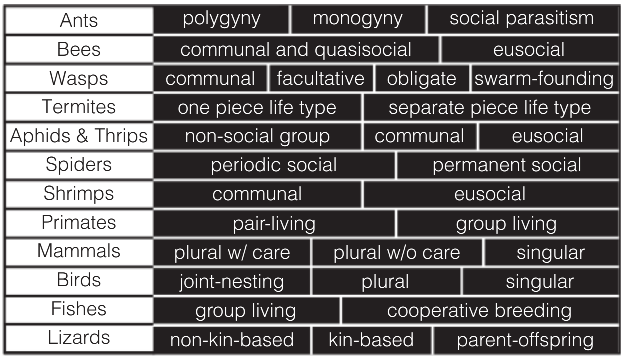
A look back over the chapters in this book shows that they clearly encompass a daunting amount of information. The goal of this concluding chapter is to begin synthesizing this information by comparing and contrasting social phenotypes within and across lineages of animals, by examining some of the social traits covered in detail in each of the other chapters of this book. We begin by exploring past efforts at social synthesis, arguing that traits of the social group should be used to describe social organization and that traits of social species be used to describe social syndromes. Building upon these past efforts, we introduce a simple categorization scheme that uses just four key social traits of the group: (1) group structure; (2) reproductive structure; (3) alloparental care; and (4) genetic structure. We next discuss two social syndromes that have been identified in recent years that link vertebrates and invertebrates: (1) central place foraging; and (2) fortress defense. We then summarize what we have learned in our readings of these chapters, emphasizing three life history traits that we believe offer the greatest potential for future comparative work: (1) longevity; (2) fecundity; and (3) developmental mode. We highlight these traits of social species because they have received a great deal of previous attention (in a variety of species), yet there is no consensus on how they broadly relate to sociality, because different measures are often used in different taxa or studies (i.e. for longevity and fecundity), or they have not been compared formally across lineages (e.g. developmental mode). We then discuss one area of social organization that appears ripe for further study: communal breeding. Communal breeders, which are common in both invertebrates and vertebrates, are ideal for tests of the origins of group living and the evolutionary transitions among different forms of social organization because of the way in which direct fitness effects of group living can be determined without the complication of derived traits such as a division of labor. Paradoxically, communal breeders are poorly studied, perhaps because they have been seen as “way stops” on the road to cooperative breeding or eusociality. We argue that a greater effort to study communal breeders and social transitions is needed to develop a comprehensive theory for complex animal sociality. Finally, we discuss how two social syndromes (i.e. central place foragers and fortress defenders) offer an opportunity to explore the monogamy hypothesis (Boomsma, 2007) and further test the idea that high genetic relatedness among offspring is essential for the evolution of eusociality, castes, and perhaps the evolution of sociality more broadly. We use Hamilton’s rule to guide much of our synthesis, and note as others have that one challenge to synthesis has been the degree to which invertebrate and vertebrate biologists have emphasized different parameters of this equation (Herbers, 2009; Elgar, 2015). In doing so, we highlight areas to be tested empirically and comparatively with further field study and new molecular tools and techniques, including a systems approach to studying social evolution.

14.2 Social Synthesis: A Trait-Based Approach

Consistent themes have emerged in our understanding of the ecological factors that shape the most derived forms of sociality in various vertebrate and invertebrate taxa (Wilson, 1975; Evans, 1977; Abe, 1991; Clutton-Brock, *et al.*, 2009; Sherman, 2013). Principle among these is that while social species may be taxonomically diverse, many share a common set of ecological and life history traits. The implication is that social species can be categorized by the social traits that they share, with the result being that there may be only two or three broad social types, or "syndromes" (Alexander, *et al.*, 1991; Crespi, 1994; Queller & Strassmann, 1998; Korb & Heinze, 2008b). But as appealing as the idea may be that social animals fit into distinct bins, these categories are hypotheses, not givens. As we describe later, the study of sociality in invertebrates and vertebrates has developed along separate traditions. This means that efforts at synthesis – including this one – inevitably paint with broad brush strokes. As all of the authors in this book emphasize, there are exceptions in every group, and still many unknowns. An important consequence of these separate traditions is that, as we discussed in Chapter 1, finding a common terminology remains a work in progress, and without one, true social synthesis remains challenging.

Finding a common terminology is no simple task. Scientists studying animal sociality love to use jargon. We use specialized terms like "pleometrosis" (i.e. colony foundation by several queens) or "supernumerary" (i.e. a helper in birds). We also use very different terms to describe the variation in social organization within disparate taxonomic groups (e.g. quasisocial, semisocial, communal, singular breeding, plural breeding, monogynous, polygynous), often for social organizations that may have at least superficially similar structures (Rubenstein, *et al.*, 2016). At the most basic level, even determining what constitutes a group varies among taxa. For example, in primates (Chapter 9), a pair is considered to be a type of group, but in birds (Chapter 11), where the majority of species form monogamous pair bonds, a social group is defined as having three or more individuals. Indeed, perhaps one of the most striking observations to be made from this book is that the attributes used to describe social organization in each taxonomic group vary greatly among chapters. Figure 14.1 illustrates the terms that each group of authors chose to use to describe the forms of sociality within their taxon. There is surprisingly little if any overlap in the terminology used to describe social organization in each chapter, even for chapters that emphasize closely related taxa (e.g. Hymenoptera or mammals). This illustrates a longstanding problem in this field: taxon-specific terminology used to define social organization often clouds attempts at social synthesis.

Part of this confusion likely stems from the type of traits that researchers use to categorize different social organizations and species. That is, some attempts at social synthesis are based upon similarities in the traits of social *species* (i.e. traits that can be measured in a single individual), whereas others are based upon similarities in the traits of social *groups* (i.e. traits that can only be quantified by looking at a group of interacting individuals). It would be useful to have a classification scheme that accounts for both types of traits. For example, "social organization" could be used to describe the



Ants	polygyny	monogyny	social parasitism	
Bees	communal and quasisocial	eusocial		
Wasps	communal	facultative	obligate	swarm-founding
Termites	one piece life type	separate piece life type		
Aphids & Thrips	non-social group	communal	eusocial	
Spiders	periodic social	permanent social		
Shrimps	communal	eusocial		
Primates	pair-living	group living		
Mammals	plural w/ care	plural w/o care	singular	
Birds	joint-nesting	plural	singular	
Fishes	group living	cooperative breeding		
Lizards	non-kin-based	kin-based	parent-offspring	

Figure 14.1 The terms that each group of authors in this book used to describe the forms of social organization within their taxon.

structure of animal societies from the traits of the groups that they form, whereas "social syndrome" could be used to describe the type or flavor of animal societies from the traits of social species. Below, after first summarizing how previous researchers have attempted to categorize different forms of animal societies with species- and group-level traits, we outline what such an organizational scheme might look like.

14.2.1 Social Organization: Social Classification Using the Traits of Social Groups

One of the first attempts to categorize different social organization was Michener's (1969) comparison of social behavior in bees. He developed a hierarchical categorization based largely upon the traits of social groups that was later modified by Wilson (1971) to separate social insect species based upon the presence or absence of castes, cooperative care of offspring, and overlapping generations. Recognizing that these same criteria described sociality in cooperatively breeding vertebrates, Sherman, *et al.* (1995) used an alternative approach to categorize social species based upon the division of reproduction within social groups. Their "eusociality continuum" idea arrayed social species along a spectrum of reproductive skew (i.e. reproductive sharing), though critics emphasized the differences in social organization more than the similarities (Crespi & Yanega, 1995). Both of these approaches categorized social species based largely upon the traits of the groups that they form. Yet, employing a completely different approach, Helms Cahan, *et al.* (2002) advocated viewing a species' social organization as the result of a series of decisions that individuals make about whether or not to disperse from their natal territory, whether to co-breed or refrain from breeding, and whether or not to provide alloparental care. This social trajectory approach was based more upon individual decision rules and traits of species, rather than upon patterns of social behaviors and traits of their groups (*sensu* Michener, 1969; Wilson, 1971; Sherman, *et al.*, 1995). It expanded upon the decision rules often used to study helping behavior in cooperatively breeding bird societies: (1) to stay or disperse; and (2) to help or not (Emlen, 1982; Dickinson & Hatchwell, 2004).

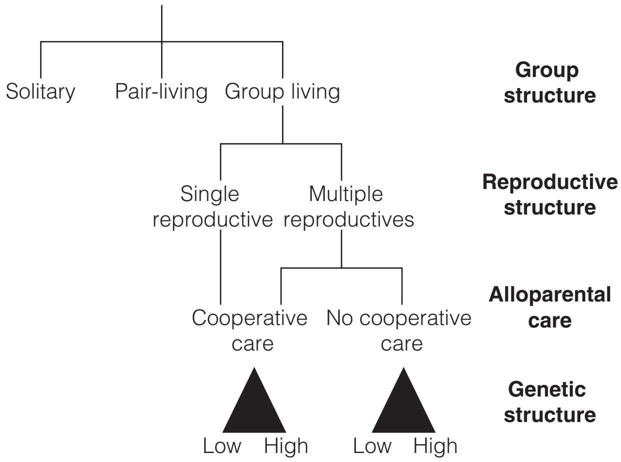


Figure 14.2 Categorization of social species using four key social traits of the group: (1) group structure; (2) reproductive structure; (3) alloparental care; and (4) genetic structure. Group structure describes whether individuals live solitarily, form a pair, or form a group (of more than two individuals). Reproductive structure describes whether one versus more than one female breeds in a group. Alloparental care describes whether individuals cooperate to care for young. Genetic structure describes the relatedness among group members, and in this context in particular, the relatedness among breeding females. The black triangles describe the range of genetics structures (from low to high) within a group.

Although these and many other authors have proposed ways to categorize variation in social organization within and among taxonomic groups, one of the clear challenges in developing a unifying framework to account for variation in social organization is that vertebrate and invertebrate biologists cannot seem to agree. As we (Chapter 1) and others (e.g. Wcislo, 1997) have noted, one reason for this may be the overabundance of terms used to describe social structure (e.g. Figure 14.1), which makes it difficult to compare and contrast across animal lineages. Figure 14.2 represents our attempt to categorize social species using four key social traits of the group: (1) group structure; (2) reproductive structure; (3) alloparental care; and (4) genetic structure. Our approach is more akin to the social trajectory approach used by Michener (1969) and Wilson (1971) to make a hierarchy of social organizations, but it also employs some of the decision rule logic adopted by Helms Cahan, *et al.* (2002) and others.

Group structure describes whether individuals live solitarily, form a pair, or form a group (of more than two individuals). Although for most species this distinction is obvious, for some it may be less clear. For example, a species of bird with bi-parental care at a nest would be considered to form a pair, but a species with uniparental care would be considered to live solitarily. Similarly, a non-eusocial species of aphid in which a single breeding female lives with her offspring in a gall prior to their dispersal would be considered to live solitarily. *Reproductive structure* describes whether one versus more than one female in a group breeds and produces offspring. Social species are typically divided into those characterized by a single breeding female per group (i.e. monogyny in insects, singular breeding in vertebrates) versus those with multiple breeding females per group (i.e. polygyny in insects, plural breeding in vertebrates) (West-Eberhard, 1978; Brown, 1987; Keller & Vargo, 1993; Keller & Reeve 1994; Solomon & French, 1997). This distinction in social organization between societies with one versus more than one breeding female may represent an important evolutionary divide in both insects and vertebrates (Rubenstein, *et al.* 2016). *Alloparental care* describes whether individuals cooperate to care for young that are not their own. Implicit in this concept of alloparental care is the idea that groups of individuals who provide cooperative care of young consist of overlapping generations. *Genetic structure* describes the relatedness among group members and, in particular, the relatedness among breeding females (i.e. whether and how related they are to each other). Genetic relatedness among group mates is influenced both by the number of female breeders in the group (i.e. reproductive structure), but also by the number of mates that each female has (Rubenstein, 2012). So while genetic structure is related to the group structure, they describe slightly different things.

Can these four traits capture the majority of the social variation across taxonomic groups? If we approach this question only thinking about the traits of the group, then we believe that they can. After all, the basic demographic and reproductive structures (i.e. numbers and patterns of breeding versus non-breeding group members) of animal societies are similar in both vertebrates and invertebrates (Rubenstein, *et al.*, 2016). For example, although all ants are eusocial, the way that colonies form and the number of queens in a colony helps distinguish among the forms of sociality in ant societies (Chapter 1). Moreover, birds and mammals are categorized by social groups with one versus more than one breeding female, but one factor that further distinguishes one form from another is whether the groups with multiple breeding pairs cooperatively care for offspring or not (Chapters 8–10). Additionally, the factors that influence the genetic structure within groups are the same for invertebrates and vertebrates: the number of breeders and the number of mates that each breeder has (Rubenstein, 2012).

It is clear that whether the breeders or other members of a group are related has important implications for levels of cooperation and conflict within the group, as well as the potential for kin-directed benefits of cooperation (Rubenstein, 2012; Boomsma, *et al.*, 2014; Rubenstein, *et al.*, 2016). So while these four social traits of the group – group structure, reproductive structure, alloparental care, and genetic structure – do not capture all of the social diversity of life, we believe that they represent a relatively simple way to classify social organization in most invertebrates and vertebrates in a unified way. Within specific taxonomic groups, species can be further sub-categorized by other group traits as taxonomic specialists see fit. More generally, however, using traits of the group to describe similarities among social species gives us a straightforward way to classify social organization in diverse taxonomic groups and across lineages. Looking forward, as more data are accumulated about a diversity of social creatures, such a scheme is a natural fit for comparative databases that compile the critical features that characterize animal societies (Starr, 2006).

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14.2.2 Social Syndromes: Social Classification Using the Traits of Social Species

Paralleling efforts by Michener and others to classify similar forms of social organization in animals based upon similarities in the traits of their groups were attempts to compare and contrast social species based upon shared ecological patterns and their general life histories (Clutton-Brock, *et al.*, 2009). This approach was based more upon the idea of using traits of social species than using traits of the groups that they form. For example, all eusocial Hymenoptera, separate type termites, and cooperatively-breeding vertebrates (except the eusocial mole-rats) are “central place foragers” (i.e. some group members forage outside of the nest or domicile, and may delay or forego reproduction altogether). Offspring within these groups may develop relatively slowly and are dependent upon parents for food and protection. And, as Evans (1977) described, a foraging solitary wasp requires basic adaptations for protecting larval brood while she is foraging (Chapter 8). At the group level, cooperative nest defense is one such mechanism for protecting offspring not only in insects (Wilson, 1971; Strassmann, *et al.*, 1988), but also in communal breeding birds (Vehrencamp, 1978). Thus, the idea is that social species share, and can be categorized by, features such as communal defense or brood care, which are themselves a consequence of a series of species-level traits that we describe further below.

Gadagkar (1990) brought together these basic life history traits of social species and proposed that a primary benefit of sociality in insects was insurance against complete reproductive failure (e.g. as would occur upon death of a solitary female that provisions and protects her young, or other such emergencies, West-Eberhard, 1975; Queller, 1989). Ecological and life history traits such as helpless offspring and long development could act as important predispositions to highly derived sociality, and that assured fitness returns provided by helping relatives could “tilt the scale” towards helping behaviors. The subsequent discovery of eusocial snapping shrimp that spend nearly their entire lives inside marine sponges only reinforced the generality of this model (Duffy, 1996). While predation may influence sociality in some vertebrate groups like birds (Poiani & Pagel, 1997) and fishes (Groenewoud, *et al.*, 2016), the association between sociality and predation risk is strongest for the vertebrate and insect species that live inside their food resources for most, if not all, of their lives.

Subsequent discoveries of sociality in insect species such as ambrosia beetles (Kent & Simpson, 1992), as well as work on the differences in social features across termites (reviewed in Korb, 2007; Korb, *et al.*, 2012; Chapter 5) and other taxonomic groups more broadly (summarized in Korb & Heinze, 2008a,b), formed the basis of Crespi (1994) and Queller & Strassmann’s (1998) proposition of a fundamental division in the organization of sociality in insects. Because all social Hymenoptera and higher termites are central place foragers with helpless offspring that are provisioned by workers and that delay or forego reproduction, the basic function of sociality in these species is to provide “life insurance” against costs and risks associated with foraging and providing care (West-Eberhard, 1975). In contrast, other social insects are “fortress defenders” that live in or near their food and have mobile offspring that require little or no provisioning, but are vulnerable to predation and parasitism because they live in aggregations from which easy escape is not possible (Crespi, 1994). This basic dichotomy in social syndromes – fortress defense versus central place foraging, or life insurance – helps to link many of the primitively eusocial invertebrate and vertebrate taxa. With the descriptions of remarkably consistent patterns of fortress defense in species such as snapping shrimps (Chapter 8), aphids and thrips (Chapter 6), polyembryonic wasps (Cruz, 1981; Chapter 4), one-piece type or wood-dwelling termites (Chapter 5), and the naked mole-rat (Kent & Simpson, 1992; Chapter 10), it is clear that these two syndromes are ecologically and taxonomically dissimilar, with decisive consequences for how social groups are organized and function (Korb & Heinze, 2008b). Moreover, these syndromes may also help link social vertebrates and invertebrates. That is, even the naked mole-rat, which is often considered eusocial, is essentially a fortress defender that lives almost entirely underground in tunnels connected to its tuber food resources (Jarvis, 1981; Alexander, *et al*., 1991; O'Rainin, *et al*., 2000).

To reiterate, however, these alternative social syndromes are hypotheses. Many authors have recognized similarities between social invertebrates and vertebrates that suggest additional syndromes could exist. For example, Andersson (1984) and later Brockmann (1997) recognized fundamental similarities in how ecological constraints shape patterns of cooperative breeding in birds and wasps. These species do not fit neatly into the central place foraging/fortress defense dichotomy: they lack true workers and tend to form small cooperative groups in which all individuals are totipotent with opportunities for both direct and indirect fitness returns from helping (Sherman, 2013). Korb & Heinze (2008b) suggested a third social syndrome that captures these features of cooperatively breeding vertebrates and wasps that Andersson (1984) and Brockmann (1997) initially pointed out. Additionally, open questions remain about how a focus upon conflict within these societies might also generate new ways to categorize sociality and introduce other ways to identify convergent social features (Hart & Ratnieks, 2004; West, *et al*., 2015). Nonetheless, the division of social species into social syndromes, or categories based upon the species-level traits that they share, has the potential to lead to breakthroughs in social synthesis, particularly in the age of genomics, as we describe below.

14.3 Opportunities for a Trait-Based Approach to Comparative Social Evolution

We have argued that taking a trait-based approach to social synthesis will allow us to make important insights into comparative social evolution. But what are those insights, and what are the opportunities for social synthesis? Below, we focus upon just three of the traits that we believe offer the greatest potential for future comparative work: (1) longevity; (2) fecundity; and (3) developmental mode. Although these traits have received previous attention, there is no consensus on how they broadly relate to sociality because different measures are often used in different taxa or studies (i.e. for longevity and fecundity), or they have not yet been compared across lineages (e.g. developmental mode). Additionally, one area of social organization that appears ripe for further study is a focus on communal breeding species. This intermediate form of social organization

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lends itself to comparative study across taxonomic groups and lineages, and opens up a broader discussion on social transitions. Finally, the two social syndromes we discussed earlier (i.e. central place foraging and fortress defense) offer opportunities to explore the monogamy hypothesis (Boomsma, 2007) and the idea that high genetic relatedness among offspring is essential for the evolution of eusociality, castes, and perhaps sociality more broadly.

14.3.1 Social Traits: Life History and the Potential for Social Synthesis

A striking pattern that emerges from the chapters in this book is the degree to which the authors agree on the importance and promise of life history approaches to understanding sociality (Starr, 2006). Although it has long been noted that social groups must solve the problems of allocation and scheduling that face individual organisms (e.g. Richards, 1953; Oster & Wilson, 1978), life history perspectives on social evolution have remained consistently underdeveloped (Starr, 2006; Heinze, 2006; Chapter 3). Wilson (1971) observed that many eusocial insects occupying stable environments have a suite of traits such as longer-lived or perennial colonies, slower reproduction, and low juvenile mortality that are characteristic of species with “slow” life histories (i.e. k-selected, in contrast to the “fast” life histories of r-selected species, with shorter lives and faster reproduction, Promislow & Harvey, 1990; Starr, 2006; Dobson, 2007). Social animals may thus be those predisposed towards characteristic life histories, and exhibit similar responses to the mechanisms of density regulation (Pen & Weissing, 2000; Tsuji, 2006), parental care in the context of multiple bouts of reproduction within nests (Trumbo, 2013), or spatial structures that favor kin interactions (Lion, *et al*., 2011). As tantalizing as these ideas may be, broad theoretical perspectives on insect life cycles remain notoriously challenging (Tsuji & Tsuji, 1996), and empirical patterns in life history may not always prove to have much explanatory power (Schwarz, *et al*., 2006). In vertebrates, the trend of linking studies of sociality with those of life history has a longer history, and consequently many of the ideas are more developed than in insects (Horn & Rubenstein, 1978). We briefly focus upon three life history traits that stand out in our synthesis among taxonomic groups (summarized in Table 14.1) and offer potential for future comparative work: (1) longevity; (2) fecundity; and (3) developmental mode.

Researchers studying cooperatively breeding vertebrates noted that social vertebrates exhibit life history and demographic traits that differ from their non-social counterparts (Brown, 1987; Hatchwell & Komdeur, 2000). In cooperatively breeding birds, the life history hypothesis is one of several related ideas that link life history traits such as longevity and fecundity to sociality. These hypotheses were derived from empirical observations that cooperative breeding in birds is associated with factors that cause habitat saturation (e.g. reduced adult mortality) and reduce the cost of helping relative to dispersing and breeding independently (Horn & Rubenstein, 1978). For example, sociality is associated with longer life spans and reduced clutch sizes in a number of avian cooperative breeders (Arnold & Owens, 1998; Cockburn, 1998). However, recent comparative analyses have indicated that the patterns derived from earlier studies are

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Table 14.1 Summary of key life history traits in the taxonomic groups discussed in this book. In some cases, little or no data are available, and for all traits where data are available on diversity within taxonomic groups, exceptions can be common.

	Life span/longevity	Fecundity	Developmental mode
Ants	queens longer-lived relative to workers or non-social insects; queens longer lived in monogynous species than polygynous species	high fecundity in queens; higher individual fecundity in monogynous than polygynous colonies;	holometabolous
Bees	queens longer lived than workers or non-social insects	higher in social than non-social species	holometabolous
Wasps	queens longer lived than workers or non-social insects	higher in social than non-social species	holometabolous
Termites	breeders longer-lived than non-breeders, particularly in separate type species	physograstric queens common; fertility of both primary male and female reproductive extremely high; lower in one piece life species (small colonies) and higher in separate type species (large colonies)	hemimetabolous; relatively slow juvenile development in presence of reproductives
Aphids & Thrips	galling phase tends to be longer-lived in social than non-social species, implying breeders longer-lived than those in non-social species; no data on reproductive life spans	lower in eusocial species relative to non-social species	hemimetabolous; social aphids tend to express slow juvenile development; longer gall duration in thrips
Spiders	social species may take longer to develop	lower in social species than non-social species	hemimetabolous-like; social species with slow juvenile development
Shrimps	unknown	lower in eusocial than non-eusocial species	eusocial with crawling larvae that delay dispersal; non-social with planktonic larvae
Primates	positive correlation between longevity, body size and brain size; sex expressing parental care longer lived than non-caring sex	fertility inversely related to body size	slow, extended juvenile development
Non-primate mammals	no relationship between cooperative breeding and maximum longevity	general trends of higher fecundity with group size and body size	cooperative breeders tend to have slow developing offspring requiring extended parental care
Birds	annual survival higher in cooperative breeders; cooperative breeders are longer lived than non-cooperative breeders	possible trend of smaller clutch sizes in cooperative breeders	cooperative breeding more common in species with altricial offspring

Table 14.1 (*cont.*)

	Life span/longevity	Fecundity	Developmental mode
Fish	anecdotal evidence that social species are longer lived	anecdotal evidence of lower fecundity in social species	late maturation in cooperatively breeding species
Lizards	kin-based sociality and/or monogamy associated with increased longevity	lower fecundity in social species	*Egernia* tend to have late maturing offspring

either more ambiguous than previously thought (Blumstein & Møller, 2008; Beauchamp, 2014), or in need of more detailed study (Downing, *et al.*, 2015). Moreover, in mammals, it is unclear if there is any broad association between longevity and sociality (Lukas & Clutton-Brock, 2012). Indeed, sociality is just one of many ways of reducing adult relative to juvenile mortality that might favor repeated breeding and long life, so it is in some ways not surprising that these relationships vary among taxa.

There remains a surprisingly slow integration of life history perspectives on longevity and social evolution in insects (Bourke & Franks, 1995; Kipyatkov, 2006). The life cycles of eusocial Hymenoptera and termites exhibit clear associations between patterns of colony growth (i.e. single versus multiple bouts of reproduction) and means of colony founding (i.e. independent founding by single breeders and monogyny versus dependent founding by swarms of breeders and polygyny) (Keller, 1991; Starr, 2006). Insects also clearly exhibit trade-offs among these and other life history traits. Colony founding is a vulnerable period in any insect lifecycle. The survival advantages of large body size may underlie a trade-off in ant queen size at colony foundation and queen number (Wiernasz & Cole, 2003). However, some highly derived eusocial insects defy life history rules by not exhibiting any apparent trade-off between life history traits such as longevity and fecundity (Keller & Genoud, 1997; Remolina & Hughes, 2008; Parker, 2010). Theoretical studies have also produced contrasting predictions regarding the association between sociality and life history evolution (Kokko & Ekman, 2002; Koykka & Wild, 2015). Thus, life history traits may predispose some taxonomic groups towards sociality, but those same traits undoubtedly have evolved as a consequence of sociality in others, or simply may evolve capriciously in different insect groups (Schwarz, *et al.*, 2006).

Both kin selection and demographic models of senescence can predict either positive or negative associations between sociality and various measures of survival or longevity (Gadagkar, 1991; Bourke, 2007). Positive associations derive from either direct benefits of social groups (i.e. benefits of intergenerational transfer of resources or decreased extrinsic mortality due to helping, Lee, 2003) or inclusive fitness benefits (i.e. kin-selected extension of post-reproductive life spans, Cohen, 2004; Coxworth, *et al.*, 2015). Bourke (2007) cited a model by Carey & Judge (2001) that showed how selection for parental care can lead to reduced fecundity and lifespan extension (i.e. a slow life history) that accounts for the observed patterns in many cooperatively breeding vertebrates, including how reduced adult mortality favors ecological conditions for delayed juvenile dispersal and helping (Arnold & Owens, 1998; Hatchwell & Komdeur, 2000). However, the situation is more complicated in social insects with castes because of how breeders are protected from extrinsic sources of mortality, while workers are not only exposed to increased risk while foraging (Hartmann & Heinze, 2003; Lopez-Vaamonde, *et al*., 2009), but in cases such as the fortress defenders, are practically designed to die.

Despite arguments for kin-selected benefits to shorter life spans (Tallamy & Brown, 1999; Bourke, 2007), the overall picture is of a positive association between sociality and annual adult survival or lifespan. In primates (Chapter 9), birds (Chapter 11), fishes (Chapter 12), and lizards (Chapter 13), there is either clear or anecdotal evidence that monogamy, helping, and sociality are associated with measures of longevity. Remarkably, this pattern is mirrored in each of the invertebrate taxa discussed in this book. Indeed, even in the caste-based eusocial insects, workers tend to be longer-lived than solitary insects of similar body sizes (Table 14.1). Despite the theoretical plausibility of an association between sociality and shortened life spans (i.e. if intergenerational transfer of resources is facilitated by short adult life spans, Bourke, 2007), there is little evidence of the generality of such an association (Trumbo, 2013). Clearly, this is an area ripe for broad-scale comparative analysis across lineages and disparate taxonomic groups, though as we learned in each of the chapters, the way lifespan or longevity is quantified in different taxa is often very different. Even within just the birds, for example, researchers cannot agree how to quantify longevity, and using different measures of mean versus maximum lifespan can lead to very different conclusions (Blumstein & Møller, 2008; Beauchamp, 2014; Downing, *et al*., 2015). Thus, before we can conduct true, broad-scale comparative analysis of the relationship between social behavior and lifespan across different taxonomic groups or lineages, researchers first need to be clear about how to quantify and measure longevity in different species.

The relationship between sociality and fecundity is less clear even than the relationship between sociality and longevity. Although there is evidence that cooperative breeding is associated with reduced fecundity in primates (Chapter 9), birds (Chapter 11), lizards (Chapter 13), spiders (Chapter 7), aphids and thrips (Chapter 6), shrimps (Chapter 8), and anecdotally, fishes (Chapter 12), the opposite is true in the advanced eusocial Hymenoptera (Chapters 2–4) and higher termites (Chapter 5). The reasons for these taxon-specific differences are complex, but they are likely related to the disruptive effects of the division of labor and extreme reproductive skew on fecundity/longevity trade-offs between breeders and non-breeders. Moreover, not only does it remain unclear, and even somewhat controversial, how fecundity evolves in social animals, whether fecundity is even a cause or consequence of being social has proven difficult to disentangle (Härdling & Kokko, 2003; Koykka & Wild, 2015). On the one hand, low fecundity may predispose species towards helping, but on the other, helping should have a positive effect on fitness. Additionally, conflicts of interest between breeders and non-breeders may also contribute to variation in the effects of sociality on fecundity (Bourke, 2007). Many of the species discussed in this book offer precisely the kind of variation required for phylogenetically-informed tests of the relationships between life history traits such as body size, fecundity, and longevity across multiple origins of sociality.

Another theme that emerges from the book is that developmental mode is a defining social trait in many taxonomic groups. For example, in some groups like the shrimps (Chapter 8), the mode of development differs between eusocial and non-eusocial species, where the former develop as crawling larvae that remain in the host sponge and the latter as planktonic larvae that disperse in the water column. Similarly, slow development in termites may be a driver of sociality in this group (Chapter 5). More generally, differences in the mode of development among insect taxa may at least partially explain differences in the form of social organization that a species adopts. For example, in holometabolic species with complete metamorphosis, offspring are altricial, and in holometabolic social insects, they require care, either parental or alloparental. In contrast, in hemimetabolic species with incomplete metamorphosis where offspring resemble adults, offspring are precocial and generally do not require active provisioning (Korb, 2008). This distinction in the mode of development may be particularly important in the evolution of eusociality, and possibly in the evolution of cooperative breeding as well.

Although vertebrates show different patterns of development from insects, developmental mode may also be related to sociality in birds. Vertebrate offspring show gradual development like the hemimetabolic insects, but many also need extended parental or alloparental care like the holometabolic insects. In birds, cooperative breeding occurs more frequently in altricial species (i.e. young are undeveloped and require care and feeding) than precocial species (i.e. young are mature and capable of movement after birth) (Cockburn, 2006). Altriciality in birds has been argued to play a key role in the evolution of cooperative breeding behavior because transitions to cooperation occur more frequently in altricial lineages (Ligon & Burt, 2004), though complex alloparental care still occurs in some precocial species (Hatchwell, 2009). Part of the relationship between mode of development and sociality may relate to ecology and the costs of rearing young. For example, early hypotheses for the evolution of cooperative breeding in vertebrates suggested that costs of rearing young in harsh environments promoted sociality (Emlen, 1982; Koenig, *et al*. 2011, 2016). Indeed, this hypothesis may at least partially explain the broad-scale patterns of sociality in birds where cooperatively breeding species occur in more temporally variable and unpredictable environments than non-cooperatively breeding species (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011). Ultimately, further comparative studies in both insects and vertebrates are needed to understand if differences in the form of social organization within and among taxonomic groups (and/or different social syndromes) are related to how young develop. Comparing and contrasting holometabolic and hemimetabolic species, as well as altricial and precocial species, offers one promising area for synthesis across lineages. In particular, exploring how these and other traits relate to the social syndromes described above, as well as to ecology, will be informative.

14.3.2 Social Organization: The Importance of Communal Societies

We often tend to study the most derived forms of sociality in the taxonomic groups in which we work. Yet, the “less” social species may offer great potential for understanding not only how sociality evolves, but also if it evolves in similar ways across taxa. A term that occurs repeatedly – though is used inconsistently – in the literature and even more so in the chapters of this book is the word “communal” (e.g. Chapters 4, 6, 8, 10 and 11). In this book, “communal” is used in both vertebrates and invertebrates to describe very different types of animal societies. In general, however, the word communal is used to describe societies in which multiple females (often unrelated to each other) breed in the same domicile, but – at least in invertebrates – without cooperative care (e.g. various bees, wasps, shrimps, and thrips). We note, however, that in vertebrates – both birds (Brown, 1987) and mammals (Solomon & French, 1997) – communal breeding often involves some form of communal care of young, much like quasisociality in insects (Michener, 1969). Nonetheless, this distinction between cooperative offspring care, or the lack-there-of, in eusocial versus communal species appears to be an important one, particularly in the insects.

Studying communal breeding species offers the opportunity to examine intermediate steps in the evolution towards eusociality and other derived forms of sociality. As Korb & Heinze (2008b) pointed out, thinking about evolutionary transitions towards eusociality may be as important as studying the social endpoints. Although they argued for thinking about transitions between social syndromes, understanding transitions between different forms of social organization is also important. This approach harkens back to the ideas of Michener (1969, 1974) and the parasocial route to eusociality in insects, and of Emlen (1995) and Emlen, *et al.* (1995) and the extended family model of sociality in vertebrates. Both of these ideas examined transitions – or the lack thereof – between different forms of social organization. Empirical tests of these ideas have been limited, but evidence from bees suggests that eusociality and communal breeding represent different evolutionary endpoints (Wcislo & Tierney, 2009; Chapter 3). These alternative social trajectories may be common in social vertebrates and invertebrates alike (Rubenstein, *et al.* 2016). Ultimately, thinking about the role of communal species in the evolution of higher forms of social organization may be informative if we are to understand how advanced social species evolve.

14.3.3 Social Syndromes: From Hamilton’s Rule to Fortress Defense and Central Place Foraging

More than any other theoretical framework of social evolution, inclusive fitness theory generally, and Hamilton’s Rule specifically (*r*b more than c; Hamilton, 1964), has guided empirical studies of social vertebrates and invertebrates alike, though with an emphasis on different parameters of the equation in the different lineages (Elgar, 2015). Comparative analyses of the costs and benefits of sociality emerged early from the study of vertebrates (Crook, 1964; Lack, 1947). Decades of empirical work on cooperatively breeding birds and mammals tended to emphasize these constraints on independent breeding (e.g. Emlen, 1982; Stacey & Koenig, 1990; Koenig, *et al.*, 1992; Koenig & Dickinson, 2016) as well as the benefits of grouping (e.g. Alexander, 1974; Stacey & Ligon, 1991). In contrast, early work on invertebrates focused more upon issues of sex allocation and conflict in the haplodiploid societies of the Hymenoptera, and

Cambridge University Press
978-1-107-04339-8 — Comparative Social Evolution
Edited by Dustin R. Rubenstein , Patrick Abbot
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how relatedness resolved problems of freeloaders and sterile workers (Trivers & Hare, 1976).

Over the past few years, the taxonomic divide over which parts of Hamilton's Rule are most often tested empirically in different lineages has begun to blur, as studies of vertebrate sociality continue to emphasize relatedness more, and those of invertebrate sociality tend to emphasize ecology more. For example, a renewed focus on the role that lifetime monogamy has played in the evolution of eusociality (Boomsma, 2007, 2009, 2013) has led to testing of the relationship between sociality and polyandry/promiscuity comparatively in both insects (Hughes, *et al.*, 2008) and vertebrates alike (Cornwallis, *et al.*, 2010; Lukas & Clutton-Brock, 2012). At the same time, comparative studies relating environmental factors to the evolution of sociality in birds (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011) have generated parallel studies in Hymenoptera (Kocher, *et al.*, 2014; Purcell, *et al.*, 2015; Sheehan, *et al.*, 2015).

Despite great interest in the monogamy hypothesis in different taxonomic groups (e.g. Hughes, *et al.*, 2008; Cornwallis, *et al.*, 2010; Lukas & Clutton-Brock, 2012), various difficulties and shortcomings have been pointed out in insects (Nonacs, 2014), mammals (Kramer & Russell, 2014), and birds (Dillard & Westneat, 2016). Dillard & Westneat (2016) argued for taking a more holistic approach, and rather than focusing just upon genetic relatedness, instead suggested considering the potential covariance between the variables in Hamilton's Rule. For example, ecologically-driven covariance (i.e. the interaction between mating system and environmental variation) could also explain the relationship between monogamy and cooperation, at least in vertebrates (Dillard & Westneat, 2016). Moreover, factors other than (lifetime) monogamy influence relatedness among offspring and are undoubtedly important in the evolution of both eusociality and cooperative breeding (Rubenstein, 2012). In many eusocial species that lack a worker class, relatedness among group members is often high (sometimes even higher than 0.5), likely because of inbreeding (reviewed in Aviles & Purcell, 2012). These patterns in eusocial species with high relatedness but no true sterile worker class suggest that high genetic relatedness by itself is not sufficient for the evolution of sterile castes. In other words, the central place foragers have evolved "classically eusocial societies" defined by a true worker class, whereas the fortress defenders have evolved "primitively eusocial societies" lacking a worker class, despite often having relatedness among offspring as high as in the classically eusocial central place foragers. Thus, studying primitively eusocial, and perhaps communal, species offers an opportunity to refine our theoretical understanding of how monogamy leads to the evolution of sociality.

Ultimately, the devil is in the details when it comes to testing these ideas, and rather than glossing over lesser-studied species or those that do not fit cleanly into the framework, we suggest that they deserve particular attention. Two of the taxa that we work on (aphids and shrimps) exemplify this – neither of these primitively eusocial species fits neatly into the monogamy hypothesis framework. Eusocial and clonal aphids evolved from ancestors with low within-colony relatedness, and many non-eusocial aphids live in groups with high relatedness (Abbot, 2009; Chapter 6). Similarly, many eusocial snapping shrimps have extremely high within-colony relatedness, but workers in all species appear to be totipotent and monogamous (Chak, *et al.*, 2015;

Rubenstein, *et al., unpublished data*). We argue that focusing upon the life history differences within and between the classically eusocial, central place foragers and the primitively eusocial, fortress defenders may help to codify the monogamy hypothesis further (Starr, 2006). For example, considering the developmental differences between holometabolic and hemimetabolic species with their different forms of parental care will be informative (i.e. central place foragers tend to produce workers with larval development before breeders, whereas fortress defenders produce offspring with direct development that can grow into breeders; Table 14.1). This may represent a fundamental life history difference (i.e. life insurance against the costs of foraging and parental care) that could help drive the evolution of castes independently of genetic relatedness among offspring. Termites may make an ideal system within which to address this issue because the group contains some species that are central place foragers and others that are fortress defenders (Korb, 2007; Chapter 5). Only by studying societies other than the Hymenoptera (Costa, 2006), including communal breeders and other species with multiple breeding females (Rubenstein, 2012), can we hope to assess the generality of the monogamy hypothesis in insects, let alone in other lineages (e.g. Cornwallis, *et al.*, 2010; Lukas & Clutton-Brock, 2012). Moreover, considering the roles of ecology and other life history traits or pre-adaptations (Dillard & Westneat, 2016), as well as the roles of cooperation and conflict in influencing worker sterility (Nonacs, 2014), within the monogamy framework will also be informative. Finally, addressing this issue within the context of social syndromes may offer an ideal opportunity for true social synthesis across very different types of organisms.

14.4 Life History Traits and the Genomics Era: The Future of Comparative Social Evolution

Like much of science in the twenty-first century, the study of sociality has entered an age of genomics. As it becomes increasingly cheaper and easier to sequence and assemble complete transcriptomes (i.e. all expressed mRNA) – and even genomes – of non-model organisms (Calisi & MacManes, 2015), we are poised for a massive effort in comparative evolutionary understanding of sociality (Blumstein, *et al.*, 2010; Hofmann, *et al.*, 2014; Rubenstein & Hofmann, 2015). Yet, although it is clearly an exciting time to be working in this area, we lack a general framework for how best to do this in the genomics era. Considering both the frameworks of social organization (based upon traits of the social group) and of social syndromes (based upon traits of the social species) offers a complimentary approach to studying the molecular mechanisms underlying sociality and the social transitions towards advanced forms of sociality. For example, studies of social structure and genetic architecture in ants have shown that polygynous and monogynous colonies of the same species have distinct haplotypes whose loci occur together on a “social chromosome,” a non-combining region of the genome (Wang, et al., 2013; Purcell, *et al.*, 2014). Additionally, a forward genomic approach can be used to identify the molecular bases of social phenotypes. For example, functional genomic studies in eusocial Hymenoptera (e.g. Toth, *et al.*, 2007; Smith, et al., 2008) and termites (e.g. Terrapon, *et al.*, 2014) have identified genes and gene modules associated with different social and reproductive behaviors. Moreover, we are beginning to understand how gene regulatory networks (e.g. Bloch & Grozinger, 2011) and epigenetic mechanisms (e.g. Yan, *et al.*, 2014) influence the expression and transitions between castes and other social phenotypes. These approaches are even being applied comparatively across lineages, as conserved genetic toolkits involved in independent evolutions of social behaviors have been identified in vertebrates and insects alike (Rittshof, *et al.*, 2014).

The possibilities for comparative genomic work are seemingly endless, particularly as we expand outside of the Hymenoptera and other model organisms (Taborsky, *et al.*, 2015). One of the most important developments in the study of social insects has been the emergence of the field of "sociogenomics" (Robinson, *et al.*, 2005), which has subsequently expanded to include vertebrates (Hofmann, *et al.*, 2014; Rubenstein & Hofmann, 2015). In the coming years, sociogenomic research will bear on everything from cognition and aging to reproductive biology. The rapid emergence of new genomes of primitively social "transitional" species offers the immediate opportunity to apply completely unique perspectives on social evolution and social evolutionary transitions. For example, by sequencing ten bee genomes, Kapheim, *et al.* (2015) showed that there is no single genomic route to eusociality, and that evolutionary transitions in sociality have independent – though similar – genetic bases. Yet, as we begin to learn more about the molecular mechanisms that underlie sociality and social behavior more generally, we must first gain a better understanding of the similarities and differences in the traits that define social species. Taking a social syndrome approach based upon the traits of social species (Hofmann, *et al.*, 2014) to do this may be more informative that simply choosing model organisms or well-studied systems (Blumstein, *et al.*, 2010; Taborsky, *et al.*, 2015), as is often done in comparative studies (e.g. Rittshof, *et al.*, 2014). For example, if the classically eusocial central place foragers and the primitively eusocial fortress defenders truly represent distinct types of social syndromes, or if monogynous and polygynous species represent distinct social evolutionary outcomes, then we need to design genomic and transcriptomic studies that compare disparately related species with similar syndromes or social organizations, and these need to be coupled to studies using experimental approaches in natural populations.

From genomics to ecology, social diversity offers new opportunities for experiments and synthesis, but describing and accounting for variation in behavior and life history in natural populations remain essential. In the 1990's, easy access to molecular markers produced a technology-fueled rush of estimates of genetic relatedness within social taxa. It is worthwhile to reflect upon what we should make of those datasets today, and what collectively we learned from them. How has our understanding of the biology of social taxa changed over the past two decades, and do we interpret those genetic data in the same way now? How have the theories and concepts that motivated those studies changed? We are in the middle of another technology-fueled rush, thanks to ready access to –omics data. These data will add to the complexity of what we know about social complexity itself, and we risk being overwhelmed. To better manage the flood of data, and to be more intentional about the comparative data that we collect, we echo

Moore, *et al.* (2010) in calling for something akin to a systems approach to the study of social evolution. Such an approach would involve the integration of multiple types of data (Blumstein, *et al.*, 2010). While inevitably reducing social behavior to various data-friendly parts (e.g. a tissue-specific transcriptome), a critical element of a systems approach is that it is egalitarian in its prioritization of data: genomics does not trump ecology. Rather, as we learned from the chapters of this book, ecology not only tells us what our functional data mean for the organisms from which it derives, but knowing something about our organisms in their natural environments – how they behave and how they vary from species to species and from place to place – allows us to sew together the various parts of disparate datasets into a composite whole. This integration is the the ultimate source of new questions and new directions of study.

In summary, many of the exciting opportunities outlined here will be lost without the insights that only natural history can provide. What the authors in this volume have shown is just how promising the prospects are for the next generation of biologists who are fascinated by social behavior. It is not hard to imagine the enthusiasm that William Morton Wheeler, Alexander Skutch, Niko Tinbergen, or William D. Hamilton would have had at these prospects. We have outlined just a few agendas for comparative research in this final chapter. Within the pages of this book lie many more ideas for potential projects, Ph.D. dissertations, and research careers. Indeed, the prospects for synthetic and comparative analyses of the evolution of sociality in animals are brighter than ever.

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