
COMPARATIVE SOCIAL EVOLUTION

EDITED BY DUSTIN RUBENSTEIN
AND PATRICK ABBOT



Comparative Social Evolution

Darwin famously described special difficulties in explaining social evolution in insects. More than a century later, the evolution of sociality – defined broadly as cooperative group living – remains one of the most intriguing problems in biology. Providing a unique perspective on the study of social evolution, this volume synthesizes the features of animal social life across the principle taxonomic groups in which sociality has evolved. The chapters explore sociality in a range of species, from ants to primates, highlighting key natural and life history data and providing a comparative view across animal societies. In establishing a single framework for a common, trait-based approach towards social synthesis, this volume will enable students and investigators new to the field to systematically compare taxonomic groups and reinvigorate comparative approaches to studying animal social evolution.

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10 Sociality in Non-Primate Mammals

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Overview

Broadly defined, mammalian social behavior includes all activities that individuals engage in when interacting with conspecifics (Eisenberg, 1966). Such interactions may be agonistic or affiliative and reflect a wide array of functional contexts, including – but not limited to – foraging, predator defense, mate choice, reproductive competition, and parental care. Indeed, these social interactions are a central feature of the biology of all mammals (Lukas & Clutton-Brock, 2013). Sociality – defined as the degree to which individuals live with conspecifics in groups or societies (Eisenberg, 1966) – varies markedly across mammalian species. Sociality shapes multiple aspects of the mammalian phenotype, including mating and breeding success (Silk, 2007), physiology (Creel, 2001), and neurobiology (Fleming, *et al.*, 1999; Carter, 2003; Hofmann, *et al.*, 2014; Young & Wang 2004). These effects are evident over ecological and evolutionary time scales, indicating that social behavior is a powerful selective pressure.

Sociality is widespread, occurring in all major lineages of non-primate mammals. Among metatherians (marsupials), sociality is found primarily in the Diprotodontia (kangaroos, wallabies, and wombats) (Jarman, 1991). Among eutherians (placentals), sociality is well-documented in the Cetacea (whales and dolphins, Connor, 2000), Hyracoidea (hyraxes, Hoeck, *et al.*, 1982), Proboscidea (elephants, Moss, *et al.*, 2011), Perissodactyla (odd-toed ungulates, Cameron, *et al.*, 2009; Sundaresan, *et al.*, 2007), Cetartiodactyla (even-toed ungulates, Clutton-Brock & Guinness, 1982; Coté & Festa-Bianchet, 2001; Jarman, 1974), and Lagomorpha (rabbits, hares, and pikas; Chapman & Flux, 1990). Although members of these taxa have greatly contributed to our understanding of mammalian cooperation, communication, grouping and dominance, here we focus primarily upon the social members of three prominent orders of non-primate mammals: the Carnivora, the Rodentia, and the Chiroptera. First, collectively these three orders represent more than 70 percent of extant mammal species (Wilson & Reeder, 2005). Second, because these lineages include many of the best-studied species of social

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mammals, they offer rich opportunities to explore variation in social structure. Third, because each of these orders contains multiple social species, they allow for informative comparisons of behavior across multiple taxonomic scales.

To characterize sociality in these lineages, we begin by reviewing the leading hypotheses developed to explain why groups form. We then explore variation in the life history traits characterizing social non-primate mammals to explore whether group living is associated with particular suites of such variables. Finally, we outline the major empirical and conceptual advances emerging from studies of these social systems. For each topic, we summarize existing data and identify areas in which our understanding of mammalian social structure is lacking to stimulate further study of the causes and consequences of variation in mammalian sociality.

I SOCIAL DIVERSITY

Non-primate mammals vary enormously with respect to the nature and frequency of interactions with conspecifics, with social species as well as those that form only temporary aggregations or that lack structured social relationships (Eisenberg, 1966). We focus upon species in which individuals belong to groups and interact with group members in ways that are distinct from interactions with non-group mates. Within groups, individuals tend to communicate extensively with one another and to engage in specialized forms of cooperation and conflict such as alloparental care and reproductive competition, respectively. Living with conspecifics is expected to generate a distinct suite of environmental conditions that may impact multiple aspects of individual phenotypes. Accordingly, we consider not only the nature of social structure but also the selective forces giving rise to and resulting from the tendency for members of some species of carnivorans, rodents, and chiropterans to live in groups.

10.1 How Common is Sociality in Non-Primate Mammals?

Social structure has been characterized for roughly 2,500 (46 percent) of the approximately 5,400 species of extant mammals, including primates (Wilson & Reeder, 2005). The majority (approximately 70 percent) of mammalian species are solitary, meaning that adults tend to live alone and that interactions with conspecifics are limited primarily to relatively brief encounters associated with reproduction. The remaining approximately 30 percent of extant mammals are social, meaning that adults engage in some form of group living. Social species are distributed throughout the mammalian radiation and include some of the most extreme forms of social structure known among vertebrates (Sherman, *et al.*, 1995). Given its prevalence, phylogenetic distribution, and evolutionary significance, it is clear that sociality is a fundamental component of the biology of many non-primate mammals.

The Carnivora consists of approximately 300 extant species that, collectively, are global in distribution and occupy a vast range of terrestrial habitats and ecological

niches (Wilson & Reeder, 2005). Group living evolved multiple times from a solitary ancestral state, with recent estimates of up to 25 percent of extant carnivoran species recognized as social (Dalerum, 2007). Because social systems are complex, Smith, *et al.* (2012a) developed composite “cooperation scores” to provide a species-level index of the occurrence of none (score = 0) to all (score = 5) of the following forms of cooperation: (1) alloparental care; (2) group hunting; (3) intra-group coalitions; (4) inter-group coalitions; and (5) predator protection. Based upon this analysis, carnivorans engage in 0 to 5 forms of cooperation (mean score = 0.8 ± 0.1 ; $N = 87$ species), with alloparental care being most common (Figure 10.1). The occurrence of cooperation varies among families. For example, cooperation is rare in ursids (bears), mustelids (weasels), and most felids (cats), with a few notable exceptions such as the African lion (*Panthera leo*) (Figure 10.2). Cooperative behavior also occurs in hyenids (hyenas) and is particularly pronounced among canids (dogs) and herpestids (mongooses), with the African wild dog (*Lycaon pictus*) engaging in all five forms of cooperation.

The Rodentia includes approximately 2,000 extant species, making it the largest order of mammals (Wilson & Reeder, 2005). Accordingly, the Rodentia encompasses a vast array of social systems. Examples range from strictly solitary pocket gophers (Geomyidae) to eusocial naked mole-rats (Bathyergidae) (Lacey & Sherman, 2007). More generally, sociality among rodents ranges from short-term seasonal aggregations to life-long social groups. Social structure has been studied for at least a few species in each major sub-lineage of rodents, with the best-studied taxa being the ground-dwelling sciurids (ground squirrels) and bathyergids (African mole-rats). Although an index comparable to that of Smith, *et al.* (2012a) has not been applied to rodents, Blumstein & Armitage (1998) established a metric of social complexity for sciurids based on the number of age-sex roles within social groups such that species with the greatest diversity of roles are most complex. Values for this metric varied considerably within and among the genera *Cynomys* (prairie dogs: 1.05 ± 0.06 , from 0.84 to 1.23) and *Marmota* (marmots: 1.12 ± 0.15 , from 0.27 to 1.46) as well as the genera *Spermophilus* and *Otospermophilus* (ground squirrels, formally known simply as *Spermophilus*: 0.42 ± 0.03 , from 0.26 to 0.65). Ongoing research is revealing remarkable diversity in the social structures of the Cavimorpha, a large, highly diverse sub-order of rodents that occurs in South America and parts of Africa; recent estimates indicate that more than 50 percent of the approximately 240 recognized species of caviomorphs are social.

The Chiroptera is second only to the Rodentia in taxonomic breadth, with more than 1,200 species currently recognized (Wilson & Reeder, 2005). Although poorly studied, bats are thought to be among the most socially complex lineages of non-primate mammals (Kerth, 2008). While no quantitative overview of the nature or frequency of sociality is available for this order, group living appears to be widespread. Group sizes range from dozens of individuals to several million bats per roost or colony, although the latter arguably represent aggregations rather than behaviorally cohesive social groups (Kunz, 1982). There is a clear need for additional study of the social structures of roosting colonies, particularly given that one of the most striking aspects of chiropteran social structure is the tendency for individuals to engage in complex forms of cooperation despite spending substantial time away from group mates (Kerth, 2008).

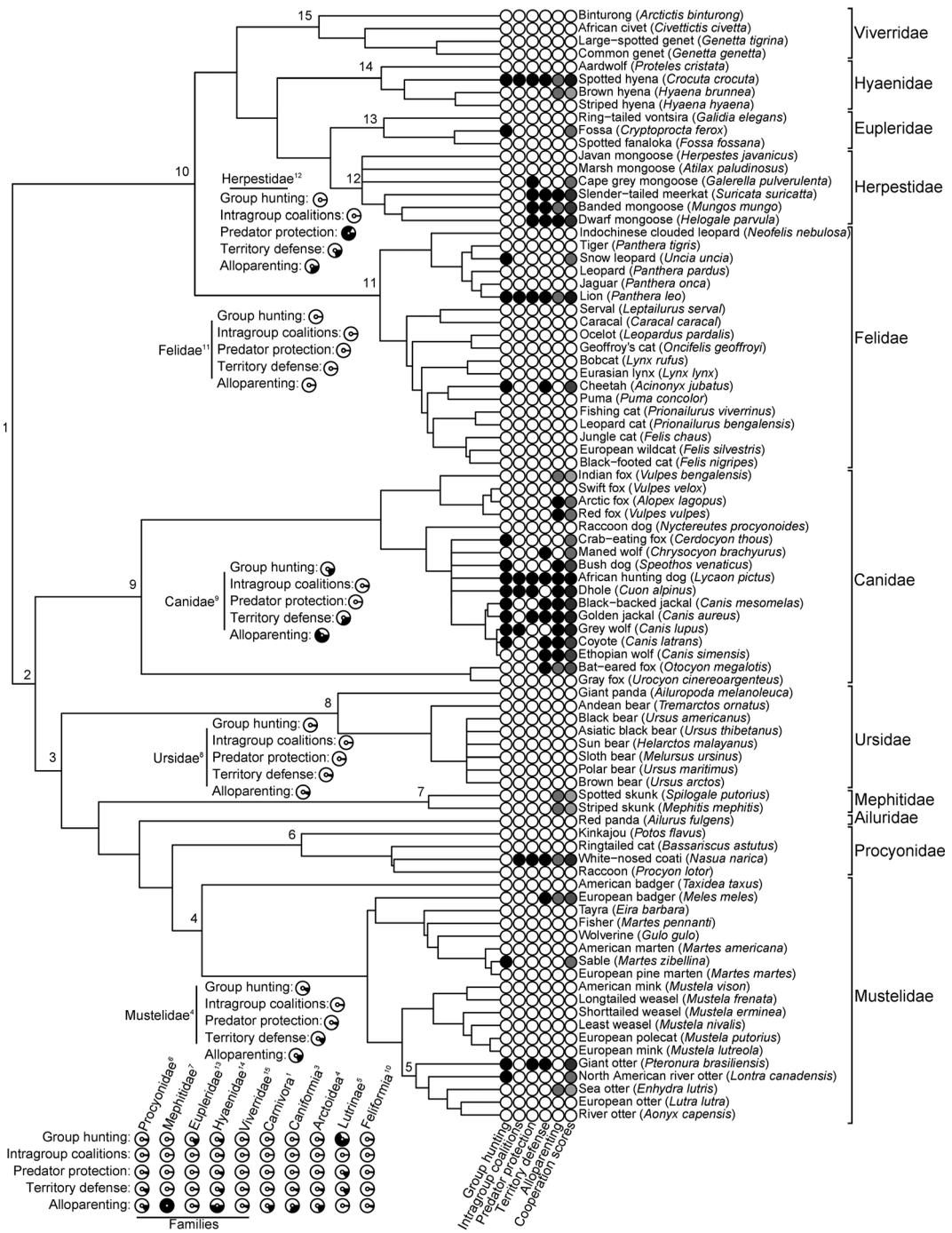


Figure 10.1 Phylogeny of extant carnivorous species for which data regarding five forms of cooperation were available. Tip labels display species names. At tips of the phylogeny are circles shaded to varying degrees indicating for each cooperation variable whether or not the species exhibits the trait. Black indicates trait presence, whereas white indicates that the species does not exhibit that trait. For alloparenting, grey indicates communal denning. Circles for the continuous variable of overall cooperation scores are shaded, with darker shading indicating higher cooperation scores for the species. Pie charts are given for each binary variable for select taxonomic groups giving the probabilities that a common ancestor was uncooperative (white) or cooperative (black). Superscripts for each taxonomic grouping refer to labeled nodes on phylogeny (reprinted from Smith, *et al.*, 2012).

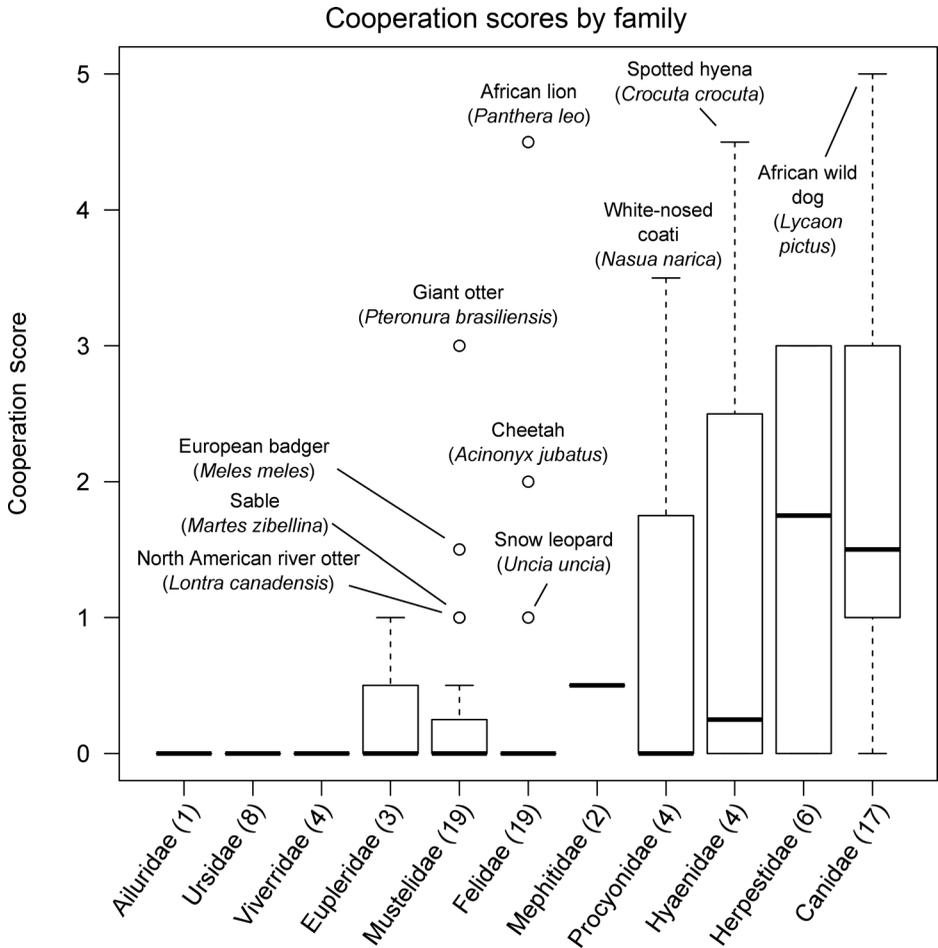


Figure 10.2 Cooperation scores among and within families of Carnivora. Dark horizontal lines in box plots represent medians, with boxes spanning the middle 50 percent of the data for each family. Whiskers stretch to any values that are outside boxes but within 2.5 quartiles from the median. Families are ranked by mean cooperation scores from least cooperative to most cooperative (left to right). Outliers within each family are those values greater than 2.5 quartiles away from the median, and are indicated by solid circles (reprinted from Smith, *et al.*, 2012).

10.2 Forms of Sociality in Non-Primate Mammals

Mammalian social groups vary considerably with respect to multiple parameters, including size, longevity, sex and age composition, kin structure, breeding structure, and degree of cooperation among group members (Krause & Ruxton, 2002; Ebensperger & Hayes, 2008). With respect to breeding structure, non-primate mammals exhibit singular breeding (i.e. one female monopolizes direct reproduction and non-breeders provide alloparental care) and plural breeding (i.e. multiple females in a group breed),

each occurring with and without communal care of offspring (Silk, 2007; Chapter 1). These elements of behavior tend to be correlated, resulting in evolutionarily important emergent trends in social structure (Lacey & Sherman, 2007). For example, large groups that form when individuals follow temporally variable food resources; tend to be short-lived and to be composed of aggregations of unrelated individuals. Within these aggregations, all adults are reproductively competent (i.e. no reproductive skew *sensu* Vehrencamp, 1983) and individuals rarely cooperate with one another (e.g. blue wildebeest, *Connochaetes taurinus*, Thirgood, *et al.*, 2004; otherwise solitary species of carnivorans, MacDonald, 1983). In contrast, groups that form when ecological conditions preclude natal dispersal tend to be considerably smaller, to persist longer, and to be composed of close kin; within these groups, individuals often cooperate extensively and reproduction may be restricted to only a subset of adults of each sex (e.g. meerkats, *Suricata suricatta*, Clutton-Brock, *et al.*, 2001). Societies with fission-fusion dynamics are characterized by individuals or subsets of group-mates that regularly merge and subdivide (Smith, *et al.*, 2008); social relationships endure without constant close proximity among group members. In general, the breeding structures of social non-primate mammals are assigned to one of four categories based on the combination of degree of reproductive skew within groups and the presence of alloparental care (Hayes, 2000; Silk, 2007; Ebensperger, *et al.*, 2012; Lukas & Clutton-Brock, 2012; Chapter 1). The resulting categories are as follows:

10.2.1 Plural Breeders without Communal Care

In plural breeding societies without communal care of offspring, all group members reproduce but care of offspring is not shared among group mates (i.e. no alloparental care occurs). This breeding structure appears to be relatively rare among social mammals, having been reported for fewer than a dozen non-primate species, including yellow-bellied marmots (*Marmota flaviventris*, Blumstein & Armitage, 1999) and spotted hyenas (*Crocuta crocuta*, Holekamp, *et al.*, 1996). For example, yellow-bellied marmot groups consist of several related breeding females and their offspring (Blumstein & Armitage, 1999). Although communal nursing occurs in some groups of marmots, communal care is not a consistent feature of the breeding structure of these animals.

10.2.2 Plural Breeders with Communal Care

In plural breeding societies with communal care, all group members reproduce and care of offspring is routinely shared among group mates. This is relatively common, occurring in more than 30 species. Among carnivorans, this list includes Artic foxes (*Alopex lagopus semenovi*), European badgers (*Meles meles*), banded mongooses (*Mungos mungo*), lions, and white-nosed coati (*Nasua narica*) (Silk, 2007; Ebensperger, *et al.*, 2012; Lukas & Clutton-Brock, 2012). Among rodents, plural breeding often involves communal nursing, in which mothers share milk with non-descendent offspring (Hayes, 2000); this type of social structure occurs in phylogenetically diverse

species found in Africa (common gundi, *Ctenodactylus gundi*), Asia (great gerbil, *Rhombomys opimus*), Europe (dormouse, *Glis glis*), North America (black-tailed prairie dog, *Cynomys ludovicianus*; Gunnison's prairie dog, *C. gunnisoni*; arctic ground squirrel, *S. parryii*) and South America (cavies, *C. porcellus*, *Microcavia australis*; colonial tuco-tucos, degus). Because groupmates in many of these societies share a communal nest or den site, other potential forms of alloparental care include thermo-regulation and defense of young from predators; among lions, alloparenting includes protection against infanticide by conspecific males (Packer, *et al.*, 1990, 2001). Although parentage assignment studies for bats lags behind those for rodents and carnivorians, data from several well-studied species such as Mexican free-tailed bats, *Tadarida brasiliensis*, and evening bats, *Nycticeius humeralis*, suggest plural breeding and communal nursing in these animals (Burland & Worthington, 2001).

10.2.3 Singular Breeders

Reproduction within groups of singular breeders is restricted to a subset of individuals of each sex – typically one male and one female – with alloparental care provided by non-breeding group members. Among non-primate mammals, this type of breeding structure is observed primarily in carnivorans and rodents (Lukas & Clutton-Brock, 2012). Among carnivorans, singular breeding occurs in canids and herpestids; in these species, non-breeding helpers of both sexes attend the den and provision the offspring of dominant breeders (Moehlman, 1986). Arguably, the best-studied singular breeder is the meerkat, in which the pronounced reproductive skew between breeding and non-breeding group members is maintained by evicting non-breeders that attempt to reproduce directly (Clutton-Brock, *et al.*, 2001, 2008; Griffin, *et al.*, 2003). In rodents, singular breeding occurs in voles (Arvicolinae), beavers (Castoridae), African mole rats (Bathyergidae), porcupines (Hystricidae), marmots (Sciuridae), Mongolian gerbils (*Meriones unguiculatus*), and several species of New World mice and rats (Sigmodontinae and Murinae) (Hayes, 2000; Ebensperger, *et al.*, 2012; Lukas & Clutton-Brock, 2012). In most singular breeding rodents, both sexes are philopatric (McGuire, *et al.*, 1993; Lacey & Sherman, 2007), with the result that females and males may act as non-breeding alloparents.

10.2.4 Eusocial Breeders

In eusocial species, reproduction within groups is restricted to a subset of individuals of each sex, typically one male and one female, with alloparental care provided by non-breeding group members. The distinction between eusociality and singular breeding is debated (e.g. Sherman, *et al.*, 1995 versus Crespi & Yanega, 1995), with potential differences between these breeding structures tied to the degree to which non-breeding alloparents retain the physiological capacity to reproduce. Only two mammal species are consistently recognized as eusocial: the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Fukomys damarensis*) (Jarvis, *et al.*, 1994; Bennett, *et al.*, 2000). Although both of these species are members of the rodent family Bathyergidae,

phylogenetic analyses indicate that eusociality has arisen independently in each species (Rowe & Honeycutt, 2002). Non-breeding mole-rats appear to retain the ability to reproduce throughout their lifetimes (Lacey & Sherman, 2007), although ecological data suggest that most individuals will never produce offspring (Lacey & Sherman, 2007).

10.2.5 Intraspecific Variation in Social Organization

Some social species of non-primate mammals do not fit readily into any single breeding structure, instead displaying intraspecific variation in social group structure. Such variation has been documented for African striped mice, *Rhabdomys pumilio*, Gunnison's prairie dogs, European badgers, and some species of *Peromyscus* mice (Schradin, 2013). The prairie vole (*Microtus ochrogaster*) is a well-documented example of a species with intraspecific variation in its social and breeding structure; this variation is evident within (McGuire, *et al.*, 2002; Solomon & Crist, 2008) and among populations (Streatfeild, *et al.*, 2011). This species is particularly notable because it displays plural breeding with communal care under some conditions, but singular breeding with alloparental care under others (Hayes & Solomon, 2004; 2006). Such species – those that engage in both breeding systems – represent particularly important targets for future study.

10.3 Why Non-Primate Mammals Form Social Groups

Social behavior has significant fitness consequences for individuals. Sociality is expected to occur when the benefits of living with conspecifics exceed the associated costs (Alexander, 1974; Krause & Ruxton, 2002). Benefits of group formation are numerous but generally encompass elements of resource acquisition, predator avoidance, offspring care, or physiological homeostasis. Typical costs include resource competition and susceptibility to pathogen transmission. The specific nature and exact magnitude of each clearly varies among taxa. Given the extended period of maternal care that characterizes many mammals, milk “theft” and misdirected care distinguish this clade from other animals (Hayes, 2000; Bordes, *et al.*, 2007). Such costs are critical in determining the consequences of group living. Because they are expected to vary with behavior, demography, and ecology, their impacts on social structure warrant careful study. Below, we consider the proposed benefits of sociality to mammals in more detail.

10.3.1 Resource Acquisition and Use

As originally described by Alexander (1974), group living is predicted to increase an individual's access to critical resources when the spatial distribution of those items requires that conspecifics aggregate in the environment. More generally, access to spatially or temporally variable resources plays an important role in the formation of

social groups in numerous mammal species; this idea has been formalized as the “resource dispersion hypothesis” (MacDonald, 1983). Specifically, when key trophic resources are patchily distributed, mammals such as European badgers, might share portions of the habitat with little or no net cost due to competition for that resource. Similarly, clumped resources promote group living at roost sites in some species of bats (Kerth, 2008), select pupping beaches in some marine carnivorans (e.g. Galápagos sea lions, *Zalophus wollebaeki*, Wolf, *et al.*, 2007) food resources in white-nosed coatis (Gompper, 1996), watering holes in capybara, *Hydrochoerus hydrochaeris*, (Herrera, *et al.*, 2011), and African elephants, *Loxodonta africana* (Grainger, *et al.*, 2005). The specific resources in question vary but members of these species share the tendency to benefit from group formation at key resources.

Resource acquisition, rather than resource dispersion *per se*, may also favor sociality in non-primate mammals. For example, in taxa that rely on food resources that are particularly challenging to secure, cooperative hunting or foraging are often important benefits to group living. Cooperative foraging is distinct from the earlier examples of resource acquisition in that the benefits to individuals require the presence and actions of conspecifics. Forms of cooperative foraging such as group hunting have been well-studied in species of carnivorans such as lions (Packer, *et al.*, 1990), African wild dogs (Creel & Creel, 1995), spotted hyenas (Holekamp, *et al.*, 1996), and wolves, *Canis lupus* (Mech, *et al.*, 2015). In each of these taxa, cooperative hunting allows group members to capture larger prey items than would be possible for lone individuals (Smith, *et al.*, 2012). The role of cooperative foraging in promoting sociality among rodents has received less attention, although this lineage includes at least one notable example, the naked mole-rat, in which members of a social group cooperate to dig the subterranean tunnels required to reach food resources (Brett, 1991). In an apparently unique twist, vampire bats engage in reciprocal food sharing of blood meals (Wilkinson, 1984; Carter & Wilkinson, 2013).

10.3.2 Predator Avoidance

Living with conspecifics often decreases the risk of predation by increasing the likelihood that threats are detected and creating opportunities for cooperative defense against predators (Ebensperger, 2001). As with access to spatially or temporally patchy resources, the reduced risk that any given individual will be depredated when in a large group (i.e. the “dilution effect,” Foster & Treherne, 1981) requires only the presence of conspecifics. In contrast, benefits resulting from cooperative defense and, in some cases, increased predator detection, require the active participation of group mates. For example, cooperative defense by small carnivores involves coordinated deterrence of predators (Smith, *et al.*, 2012). In multiple species of rodents, improved predator detection involves vigilance and alarm calling (e.g. Blumstein, 2007). In some taxa, this enhanced vigilance has been shown not only to increase predator detection but also to allow group members to allocate more time to other direct fitness enhancing activities such as foraging (FitzGibbon, 1989). Demonstrating that vigilance is cooperative can be challenging. Participation in predator detection is clearly shared among members of

some species such as meerkats, in which group members take turns acting as sentinels (Clutton-Brock, *et al.*, 1999). In Belding's' ground squirrels, *Urocitellus beldingi* (Sherman, 1977), however, alarm calling may simply be a function of which individual first detects a threat (Blumstein, 2007). Because improved predator detection often impacts both direct and indirect fitness – including simultaneously enhancing both (e.g. Sherman, 1977) – determining the exact inclusive fitness benefits of this behavior is challenging. Clearly, however, predator detection and anti-predator defense of conspecifics represent potentially important benefits to sociality in multiple non-primate mammals.

10.3.3 Homeostasis

Group living may promote physiological homeostasis, which refers to an organism's ability to maintain bodily functions within a species-typical range of values. Although all mammals generate internal heat to thermoregulate, the traits they use to conserve metabolically generated heat vary. In some species, huddling by members of social groups enhances thermoregulation; this is a benefit of group formation for multiple species of rodents (McShea & Madison, 1984; Blumstein, *et al.*, 2004) and some species of temperate-zone bats (Kerth, 2008; Ebensperger, 2001). This benefit may be particularly important to the survival of offspring in taxa with altricial young that are born helpless and requiring extensive care. Communal rearing typically decreases the amount of time that offspring are left unattended. For example, communal care allows some adult prairie voles to forage while others remain with young and help them to maintain a stable thermal environment (Hayes & Solomon, 2006), which contributes to the more rapid development of communally-reared offspring (Hayes & Solomon, 2004). Similarly, a primary factor favoring sociality in bats is their extremely demanding thermoregulatory physiology, particularly at night and during hibernation (Kerth, 2008). Many species of bats are thought to benefit from roosting socially to maintain body heat (Eisenberg, 1966). Although thermal benefits have received less attention in studies of carnivoran societies, these animals often benefit from group living in terms of increased homeostasis in communal dens (Creel, 2001).

10.3.4 Mating

Individuals that live in groups may benefit via improved access to mates; a shortage of potential reproductive partners may favor natal philopatry and thus the formation of social groups (Emlen & Oring, 1977). Mammalian mating systems are typically characterized based on the number of reproductive partners per individual and include monogamy (i.e. one male mates with one female), polygyny (i.e. one male mates with multiple females), polyandry (i.e. one female mates with multiple males), and polygynandry (i.e. multiple partners for both sexes) (Clutton-Brock, 1988). Which of these systems a species exhibits reflects a combination of ecological, evolutionary, and life history parameters that, collectively, determine the number of mates that an individual can gain access to (Emlen & Oring, 1977). For species in

which all group members reproduce (i.e. plural breeders, low reproductive skew), membership in the social group may ensure access to mates (e.g. shortage of partners elsewhere in the habitat), to a larger number of mates (e.g. male defense of multiple females), or to better quality mates (e.g. males that win competitive encounters to secure access to a group of females). For species in which breeding is limited to a subset of adults per group (i.e. singular breeding, high reproductive skew), membership in the group and the associated long-term social bonds that develop among group mates may increase the chances that an individual will eventually become a breeder within the group. Reproductive “queuing” has been suggested for dwarf mongooses, *Helogale parvula* (Creel & Waser, 1994), meerkats (Clutton-Brock, *et al.*, 2001), and naked mole-rats (Lacey & Sherman, 2007).

10.3.5 Offspring Care

In most mammals, care of offspring is performed primarily – if not exclusively – by the female parent. In some social species, however, other adults contribute to care of young; helpers may include other reproductive females or non-breeding “helpers” of one or both sexes (Hayes, 2000; Silk, 2007). Such alloparental care occurs in multiple forms. These behaviors may be divided into two types: direct care (i.e. activities that are clearly targeted toward young) and indirect care (i.e. activities that benefit all group members, including young). Examples of the former include guarding, grooming, and feeding young; examples of the latter include predator detection, cooperative foraging, and thermoregulatory benefits associated with use of a communal nest or den site (Creel & Creel, 1991; Solomon & Hayes, 2009; Lukas & Clutton-Brock, 2012). In groups containing multiple breeding females, care of non-offspring may also include allonursing of young, which has been reported for multiple species of carnivorans, chiropterans, and rodents (e.g. Packer, *et al.*, 1992; Hayes, 2000; Kerth, 2008). In many cases, however, it is unclear whether this behavior occurs because females allow non-offspring to nurse or because females lack the ability to discriminate between their own young from the offspring of others (König, 1994; Hayes & Solomon, 2004, 2006).

More generally, assessing the benefits of alloparental care requires consideration of fitness consequences for both parents and non-parents. Alloparental care is expected to enhance the direct fitness of parents and, depending upon patterns of kinship, the indirect fitness of other group members. These predicted relationships are most clearly upheld in singular breeding groups containing non-breeding alloparents; in these species, the direct fitness of breeding animals tends to increase with the number of non-breeders providing care (Silk, 2007) and alloparents tend to be closely related to the young that they assist, indicating that indirect fitness benefits are possible (Clutton-Brock, 2009). In some social species, however, these predicted fitness outcomes may be complicated by other aspects of group living, such that per capita direct fitness decreases with group size (e.g. colonial tuco-tucos and black tailed prairie dogs, Hoogland, 1995; Lacey, 2004). Moreover, not all carnivorans that engage in alloparental behavior are related to the offspring receiving care (e.g. dwarf mongooses, Creel & Waser, 1994). Thus, while care of offspring is an

important potential benefit of group living, the specific nature and magnitude of the fitness consequences of this behavior vary substantially among non-primate mammals.

10.4 The Role of Ecology in Shaping Sociality in Non-Primate Mammals

Ecology is a critical determinant of multiple aspects of social structure. Perhaps most conspicuous is the fundamental role that ecology plays in establishing the costs and benefits of group living. This includes not only competition for critical resources, but also aspects of predator defense and pathogen exposure (Alexander, 1974).

10.4.1 Habitat and Environment

Empirical studies that examine interactions between ecology and social behavior have been slow to emerge. Groups structured by fission-fusion dynamics represent one form of mammalian sociality that may prove particularly informative regarding interactions between ecology and behavior because group members regularly separate and reunite (Smith, *et al.*, 2008). Local ecological conditions both promote and constrain grouping patterns, particularly within the Carnivora; most social species of carnivorans forage in small parties to reduce feeding competition (Smith, *et al.*, 2008). Among the Rodentia, evidence that ecological factors contribute to individual dispersal decisions is limited to largely qualitative comparisons of habitat conditions in social versus solitary taxa (e.g. colonial tuco-tucos, Lacey & Wieczorek, 2004). For others, intraspecific variation in ecology and social structure reveals key ecological variables associated with natal philopatry (e.g. great gerbils, Randall, *et al.*, 2005; degus, Ebensperger, *et al.*, 2012; African striped mice, Schradin, *et al.*, 2012). The most compelling studies are those that experimentally manipulate resource availability to characterize interactions between ecology and natal philopatry (e.g. prairie voles, Smith & Batzli, 2006; Lucia, *et al.*, 2008), but such experimental studies are particularly rare. Because of the challenges associated with field manipulation of habitat parameters, carefully designed intra- and inter-specific comparisons are likely the most tractable way forward for understanding the complex relationships among ecology, dispersal patterns, and social structure.

10.4.2 Biogeography

Carnivorans, rodents, and bats are speciose groups that occur worldwide, with social taxa found throughout the geographic distribution for each lineage. Carnivorans are nearly cosmopolitan; this includes several specific families of Carnivora (e.g. Felidae, Canidae, Phocidae) that are nearly global in distribution. Geographic “hot spots” for endemic species of carnivorans include Borneo, Java and Sumatra, Madagascar, Mesoamerica, Western Ghats, and Sri Lanka, and the Guinean Forests of West Africa (Sechrest, *et al.*, 2002). Rodents are also geographically widespread, occurring on all continents except Antarctica (Honeycutt, *et al.*, 2007). Although a few families (e.g. Sciuridae) are effectively cosmopolitan, in general individual rodent clades tend to be

associated with particular geographic regions. Rodent families endemic to sub-Saharan Africa are among the oldest members of this order (Honeycutt, *et al.*, 2007), with the extensive caviomorph clade representing the oldest radiation in South America. Interestingly, 57 percent of extant rodent species are endemic to Australia, despite the general association between this continent and marsupial diversity (Honeycutt, *et al.*, 2007). The biogeography of chiropterans is similar in that, collectively, members of this order are nearly cosmopolitan. Although one family, the Vespertilionidae, spans much of the geographic distribution of the order, other families tend to be more restricted to either specific landmasses or ecogeographic regions (e.g. tropical habitats) of the world. In comparison to carnivorans and rodents, the fossil record for bats is relatively sparse, but a well-resolved molecular phylogeny for all extant families suggests that megabats are nested among four major lineages of microbats (Teeling, *et al.*, 2005). Sociality – specifically cooperative breeding – among birds is particularly prevalent in northern South America, sub-Saharan Africa, and Australia (Jetz & Rubenstein, 2011); in contrast, although no formal quantitative analyses have been conducted, sociality among mammals does not seem to be similarly associated with a particular subset of geographic regions.

10.4.3 Niches

Given their taxonomic and ecological diversity, carnivorans, rodents and bats occupy a wide range of ecological niches. Because carnivoran diets are typically comprised primarily of meat, carnivorans are important in many ecosystems as top predators that regulate the abundance of other animals (e.g. Mech, *et al.*, 2015). The highly social mongooses are a notable exception because members of this clade feed primarily on invertebrates and thus, ecologically, can be characterized as insectivorous. Social rodents are ecologically much more diverse, occurring in all terrestrial biomes and occupying subterranean, aquatic, and arboreal habitats. Rodents are primarily herbivorous and include grazers, browsers, frugivores, and root or bulb specialists. In addition to serving as important prey, some social rodents serve as ecosystem engineers by substantially altering the structure of the habitats in which they occur; social species that fill this role include beavers (*Castor canadensis*) and multiple species of burrowing squirrels. Bats occupy numerous trophic roles, including those of insectivores, carnivores, nectarivores, frugivores, and sanguinivores (Neuweiler, 1989). Accordingly, bats fulfill multiple critical ecological functions as pollinators, seed dispersers, and predators.

10.5 The Role of Evolutionary History in Shaping Sociality in Non-Primate Mammals

In addition to ecology, evolutionary history is expected to be a significant determinant of social structure in non-primate mammals. Carnivorans, rodents, and bats represent markedly divergent lineages of mammals, each of which has followed a distinct

evolutionary trajectory within the larger framework of their shared membership in the mammalian clade. Consideration of phylogenetic history has revealed that patterns of social behavior vary within each of these lineages. In the carnivorans sociality generally appears to be rare among ursids, mustelids, and felids, although several notable exceptions occur in the latter two families (Smith, *et al.*, 2012). In contrast, most canids (dogs), herpestids (mongooses), and hyenids (hyenas) are social and tend to engage in cooperative behavior (Smith, *et al.*, 2012). Among rodents, sociality is particularly prevalent within the Caviomorpha (Hayes & Ebensperger, 2011) and some families of the Sciuromorpha (e.g. sciurids, Murie & Michener, 1984; Blumstein & Armitage, 1999) but conspicuously absent in others (e.g. geomyid pocket gophers, Lacey, 2000). Within the bats, phylogenetic history fails to predict call characters used for sophisticated laryngeal echolocation; these traits are apparently highly convergent across the chiropterans (Eick, *et al.*, 2005). In contrast, the negative evolutionary relationship between male testes size and brain size apparently drives mating systems within chiropterans; female promiscuity is most common in species with the smallest brains (Pitnick, *et al.*, 2016). These strong phylogenetic patterns suggest that evolutionary history shapes social structure in concert with current environmental conditions and interspecific differences in ecology.

Evolutionary history also shapes mating structure within groups. For example, singular breeding groups evolved from monogamous ancestors (Lukas & Clutton-Brock, 2012; 2013), with the resulting close kinship among group mates enhancing the potential for indirect fitness benefits. Although it has been argued that singular and plural breeding systems represent endpoints along a continuum of reproductive structures (Sherman, *et al.*, 1995), a quantitative review of relationships between group size and breeding structure suggests that singular and plural breeding instead represent distinct forms of sociality (Rubenstein, *et al.*, 2016). Taken together, these findings imply that evolutionary history has contributed significantly to the extent to which individuals forego direct production of offspring in species of non-primate mammals.

To better understand how evolutionary history and current ecology interact to shape sociality, a growing number of studies use comparative, phylogenetically informed analyses to examine correlates of variation in social behavior. For instance, Lukas & Clutton-Brock (2012) argue that cooperative (singular) breeding is evolutionarily derived from social monogamy. This form of sociality has evolved at least fourteen times in mammals, with thirteen of the evolutionary transitions from monogamy to cooperative breeding occurring in rodents and carnivorans. Whereas sociality likely evolved within African mole-rats (Bathyergidae) due to ecological constraints on dispersal imposed by arid habitats and patchily distributed food resources (Rowe & Honeycutt, 2002), sociality in caviomorph rodents coevolved with increased body sizes and use of subterranean burrows (Ebensperger & Cofre, 2001). Unfortunately, because these studies focus on different rodent taxa, it is not possible to determine the extent to which the ecological factors identified as important to each clade (e.g. aridity, distribution of food, burrow use) may contribute to apparent differences in general patterns of social structure between bathyergid and caviomorph rodents.

II SOCIAL TRAITS

Natural selection has created correlations between multiple life history traits and elements of social structure in non-primate mammals. Here, we identify a suite of traits (e.g. forms of communication, reproductive attributes, dispersal patterns) that appear to differ systematically between social and non-social species of carnivorans, rodents, and bats.

10.6 Traits of Social Species

10.6.1 Cognition and Communication

Communication contributes to numerous elements of mammalian social structure, including social bonding, predator defense, cooperative foraging, dominance hierarchies, and reproduction. Although all mammals engage in multiple modes of communication, chemical and vocal signals are particularly important in most non-primates (Bradbury & Vehrencamp, 2011). While many solitary species have complex forms of communication (e.g. Peters & Wozencraft, 1989), social species are distinguished by the tendency to have a suite of signals that are used only during interactions with group mates (Bradbury & Vehrencamp, 2011). Given the complexity and short-term unpredictability of social relationships, communication is generally expected to be more nuanced and thus potentially more cognitively demanding in social compared to non-social species (Adolphs, 2001). Accordingly, reviewing patterns of communication in group living carnivorans, rodents, and bats should yield important insights into not only the social structures of these animals but also the selective pressures acting on their neurobiology.

Social carnivorans routinely use vocal and olfactory signals to communicate with group members (Peters & Wozencraft, 1989; Archie & Theis, 2011); contexts for these signals include recognizing individuals, assessing kinship, and fostering group cohesion, all of which are critical to the maintenance of within-group social relationships. For example, spotted hyenas distinguish between the calls produced by one versus multiple intruding conspecifics as well as to distinguish among potential partners in cooperative interactions (Smith, *et al.*, 2007, 2010, 2011; Benson-Amram, *et al.*, 2011). Members of this species also use olfactory cues present in secretions from their anal glands to convey information about sex, reproductive status, and individual identity (Drea, *et al.*, 2002). Although particularly well studied in spotted hyenas, both modes of communication are expected to be common among social carnivores (e.g. Gorman & Trowbridge, 1989).

Among social rodents, chemical signals, particularly those in urine, play important roles in territory defense, regulation of reproductive activity, and decisions regarding social and reproductive partners (Wolff & Sherman, 2007). Olfactory information may be used to recognize individuals and to discriminate kin from non-kin (Smith, 2014).

Vocal communication is also widespread among rodents and occurs in multiple contexts. For example, many species emit alarm calls in response to predators; such calls may vary depending on the level of risk and type of predator (e.g. aerial versus terrestrial predators), although it is often unclear whether calls function primarily to signal predators (e.g. pursuit deterrent signals that warn predators of detection) or to warn conspecifics (Blumstein, 2007). Vocalizations can also be crucial to mother-offspring interactions and may influence the neurobehavioral development of young (Branchi, *et al.*, 2001). For both olfactory and vocal communication, it seems likely that many examples of relevant signals have yet to be described. For example, a growing body of evidence indicates that the use of ultrasonic calls may be important during courtship and aggressive encounters (Portfors, 2007). Thus, olfactory and vocal communication play critical and apparently underappreciated roles in multiple aspects of rodent social behavior.

The cognitive demands – the underlying neurobiological complexity and processing capabilities – of communication in social carnivorans and rodents are not well understood. With regard to olfactory signals, chemical cues thought to be involved in kin recognition appear to be processed only by the olfactory bulb and thus may be cognitively less demanding than other forms of communication that require the integration of multiple brain regions (e.g. Haxby, *et al.*, 1996). To date, however, the relative cognitive requirements of processing olfactory versus auditory or other types of information remain unclear.

Among social Chiroptera, information transfer via vocal communication is particularly important and used widely for mother-offspring recognition (Safi & Kerth, 2007). In common vampire bats, *Desmodus rotundus*, vocal communication is also used among non-kin to recognize and locate the most generous food-sharing partners (Carter & Wilkinson 2016). Olfactory information may also be used to attract mates (McCrahen & Wilkinson, 2000). Among species of microbats, there is a positive relationship between social complexity, defined simply as group size, and relative brain size (Dunbar & Shultz, 2007). Although many bats live and forage in challenging physical conditions, it is the complexity of the social environment that appears to be most strongly associated with potential cognitive abilities in these animals (Kerth, 2008). Indeed, the relative difference in residual brain volume (a measure that controls for differences in body size) between bats that form pair bonds and those with other mating systems is the most striking known among vertebrates (Pitnick, *et al.*, 2006), suggesting that sociality in the form of reproductive pair bonds is cognitively demanding.

10.6.2 Lifespan and Longevity

Phylogenetically informed comparisons of carnivorans suggest that multiple life history traits are correlated with sociality and cooperation in these animals (Beckhoff, *et al.*, 1984; Gittleman, 1986; Smith, *et al.*, 2012); key variables include reduced sexual dimorphism, increased age at weaning, and increased age of first reproduction. Demographic and ecological factors that likely interact with these life history parameters

include population density, degree of social group cohesion, and prolonged hunting efforts in open habitats. Interestingly, however, neither longevity nor mass-corrected basal metabolic rate is correlated with the degree of cooperation in these taxa (Smith, *et al.*, 2012). These patterns are intriguing and efforts to determine the direction of causality of these relationships should generate exciting insights into the role of lifespan in the evolution of social structure in carnivorans.

Among rodents, sociality and communal breeding may be favored in multiple species due to high rates of mortality coupled with the often pronounced need for parental care. In particular, taxa in which young individuals face harsh seasonal conditions may benefit from the extended care made possible by group living (Arnold, 1990). With regard to reproductive parameters, Blumstein & Armitage (1998) found that social complexity (based on number of age-sex categories in a group) in ground-dwelling sciurids is linked to increased age at first reproduction, reduced litter size and increased offspring survival. With regard to body size, although Ebensperger (2001) predicted that sociality should be more pronounced among small-bodied species, an empirical review (Ebensperger & Blumstein, 2006) revealed that large-bodied species of hystricognath rodents tend to be more social. As evident from this brief synopsis, such analyses have typically not included all rodent taxa and thus it remains unclear how the general differences in life history strategies characterizing sciuriform versus hystricorh rodents, the two most speciose suborders, may contribute to patterns of sociality across this lineage.

A primary factor thought to favor sociality among chiropterans is their remarkable longevity (Kerth, 2008). Bats are extraordinarily long-lived compared to other mammals of similar body sizes (Figure 10.3), with average life spans of 5 to 10 years and maximum longevity of up to 30 or more years (Barclay & Harder, 2003; Kerth, 2008). Maternal investment is also often prolonged, with females nursing young until the latter are roughly the size of adults. This combination of factors is expected to lead to extended social relationships between adults and young, which may favor natal philopatry and thus facilitate the formation of social groups comprised of multiple generations of related females (Eisenberg, 1966).

Clearly, life history attributes play important roles in the evolution of sociality among non-primate mammals. To date, however, efforts to quantify these relationships have tended to focus on traits that are distinctive to specific sub-clades of mammals, such as the striking longevity of chiropterans. Moving forward, studies that examine the same suites of parameters across diverse mammalian taxa should prove useful in elucidating the impacts of larger patterns of life history variation in mammals. For example, recent comparative analyses of cooperatively breeding rodents, carnivorans, and primates (Lukas & Clutton-Brock, 2012) indicate that this form of sociality is associated with polytocny (i.e. production of litters of multiple young) but is not consistently linked with longevity or other forms of reproductive investment in these lineages. The apparent contradiction between this result and the findings for bats described above illustrates the potential complexity of interactions between life history traits and behavior. Together, these results underscore the need for comparative studies conducted across multiple taxonomic scales.

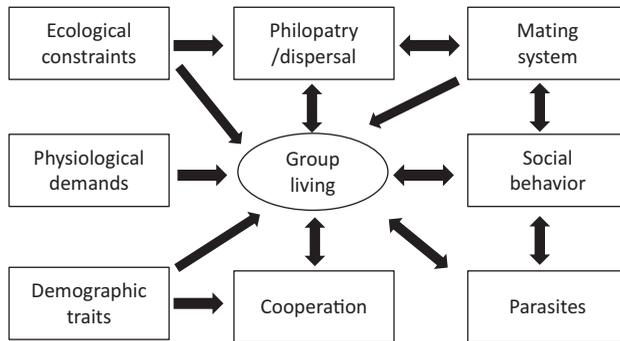


Figure 10.3 Relationships among the causes and consequences of group living in bats (redrawn from Kerth, 2008).

10.6.3 Fecundity

Fecundity, defined as the number of offspring produced by females, is an important component of fitness in all mammals. A growing body of literature suggests that individual females living in large groups and those that are more socially connected (i.e. have relationships with a greater number of conspecifics) within their social group tend to be more fecund than females that live in smaller groups or are less connected with group mates, although exceptions to these patterns do occur (e.g. badgers, Cresswell, 1992). The effects of these social parameters are layered on top of life history traits that may be strongly influenced by phylogenetic history. For example, in multiple plural (communal) breeding species of carnivorans (e.g. banded mongooses, Gilchrist, *et al.*, 2004; lions, Packer, *et al.*, 2001), age and body size are more important predictors of female fecundity than social environment. Demography may also be important, with high population density increasing within-group differences in female fecundity in some species (e.g. red deer, Clutton-Brock, *et al.*, 1987). In sum, female fecundity is clearly shaped by multiple factors, including elements of social structure, life history, and demography. Assessing the relative contributions of each of these parameters to patterns of fecundity and fitness in individual species represents an important line of research for future studies of non-primate mammals.

10.6.4 Age at First Reproduction

The age at which females first reproduce is expected to significantly impact lifetime reproductive success, since a longer reproductive lifespan should increase the number of offspring produced. Harvey & Zammuto (1985) demonstrated that the age of first reproduction is strongly influenced by life expectancy at birth. As a result, mortality schedules for juveniles are a critical determinant of several important components of female fitness, including age-specific costs and benefits of producing young and investing in parental care (Promislow & Harvey, 1990). For example, litter size and

neonatal survival of offspring generally increases with maternal age in carnivorans (e.g. common raccoons, *Procyon lotor*, red foxes, *Vulpes vulpes*) and rodents (e.g. white-footed mice, *Peromyscus leucopus*, beavers). Because group living tends to reduce rates of juvenile mortality, members of social species often initiate their reproductive careers at earlier ages than do individuals in non-social species (Promislow & Harvey, 1990). Although this outcome at first appears inconsistent with the observation that natal philopatry (a common form of social group formation) tends to be associated with delayed reproduction, it is likely that this discrepancy reflects the inclusion of plural breeding species in some analyses since delayed reproduction by philopatric animals is most typical of the subset of social species that are singular breeders (Promislow & Harvey, 1990). Thus, social structure appears to play an important role in the reproductive schedules of group living species, suggesting future studies should examine the impacts of sociality on this aspect of offspring production.

10.6.5 Dispersal

Patterns of dispersal, or conversely patterns of natal philopatry, are central to social structure in all of the mammalian taxa considered here. In most mammals, males disperse more often and tend to move greater distances than do females (Greenwood, 1980). Ecology shapes social structure through its effects on natal dispersal. Specifically, when ecological conditions render dispersal prohibitively costly, individuals may remain in their natal area, leading to the formation of social groups (Koenig, *et al.*, 1992; Hayes, 2000; Lucia, *et al.*, 2008). Ecological parameters that may contribute to high costs of dispersal include risk of predation, habitat availability, limited access to mates, and the probability of successfully rearing young in a new (i.e. non-natal) portion of the habitat (Emlen, 1994). While groups that form when conspecifics cluster around critical resources may or may not contain related individuals, groups that arise due to natal philopatry are almost necessarily composed of kin (Eisenberg, 1966; Emlen, 1994; Smith, 2014). Ecological factors are clearly central in both of these cases, but the specific mechanisms by which ecology causes conspecifics to congregate are thought to be fundamental to determining the kin structure of a group and thus the potential for direct versus indirect fitness benefits to group members (Emlen, 1994; Clutton-Brock, 2002).

Most carnivorans follow the typical mammalian pattern of male-biased dispersal. The exact conditions favoring natal philopatry and, more generally, interspecific variation in patterns and rates of movement are often poorly understood. Potential contributing factors include mating system (Greenwood, 1980; Dobson, 1982), the difficulty of hunting alone, and the extended parental care required by generally altricial carnivoran young (e.g. African wild dogs, Creel & Creel, 1995). Given the tendency for dispersal to be male-biased, social groups of carnivorans are most often comprised of closely related adult females, their offspring, and unrelated, immigrant adult males. Even in species in which some males remain in their natal group (e.g. dwarf mongooses), the extent of philopatry and thus the degree of kinship within groups tend to be greater among females, although immigrants of both sexes may occur (Lucas, *et al.*, 1994).

Dispersal among rodents is also typically male-biased (Greenwood, 1980; Dobson, 1982). Natal dispersal may be adaptive in reducing inbreeding depression, which can have negative fitness consequences, as has been reported for Belding's ground squirrels (Holekamp & Sherman, 1989) and yellow-bellied marmots (Olson, *et al.*, 2012). In the former species, male dispersal is triggered by the combination of a minimum level of body fat and circulating levels of testosterone (Nunes, *et al.*, 1998; 1999). Male-biased dispersal also occurs in most other species of ground squirrels, although it is less likely when a close female relative (e.g. mother or sibling) is absent from the natal area (Armitage, *et al.*, 2011; Hoogland, 2013), providing further suggestion that inbreeding avoidance may be important. In those species characterized by natal philopatry, ecological constraints on dispersal reflect access to critical resources, predation pressure, and the potential for cooperation to resolve ecological challenges (Lacey & Sherman, 2007, Figure 10.4). Although ecological drivers of sociality have been studied extensively for subterranean species, including African mole-rats (Jarvis, *et al.*, 1994) and tuco-tucos (Lacey, 2000), surprisingly few studies provide empirical data regarding relationships between ecology and dispersal (Lacey, 2016). Thus, future studies that quantify interactions between environmental conditions and patterns of movement to elucidate the causes of dispersal should prove informative.

As in carnivorans and rodents, dispersal in bats tends to be male-biased (Burland & Worthington, 2001). This pattern appears to be particularly characteristic of European and North American species, with more variable patterns of sex-specific dispersal occurring among tropical species (Kerth, 2008). The ecological bases for these patterns appear to vary. For example, female philopatry in Bechstein's bats (*Myotis bechsteinii*) has been linked to fitness benefits resulting from communal breeding and reduced parasite transmission between neighboring colonies (Kerth, *et al.*, 2002). In contrast, Kerth (2008) posited that male dispersal in tropical species is best explained by the benefits of avoiding resource competition among kin. These explanations are not mutually exclusive and the relative importance of factors such as parasite load and competition likely vary among taxa and geographic regions. Clearly, considerable additional research is needed to evaluate the nature, frequency, and adaptive bases for natal dispersal and natal philopatry in chiropterans.

10.7 Traits of Social Groups

10.7.1 Genetic Structure

Inclusive fitness theory predicts that animals gain important fitness benefits from living and cooperating with close kin (Hamilton, 1964). Not surprisingly, a major focus of research on sociality has been to document the kin structure of groups across diverse taxa. In general, kin structure in mammalian groups reflects the prevalence and duration of natal philopatry (Lukas & Clutton-Brock, 2012; Smith, 2014). At one extreme, groups that form when individuals cluster around critical resources may contain few related individuals, resulting in little genetic kinship within these aggregations (Ebensperger & Hayes,

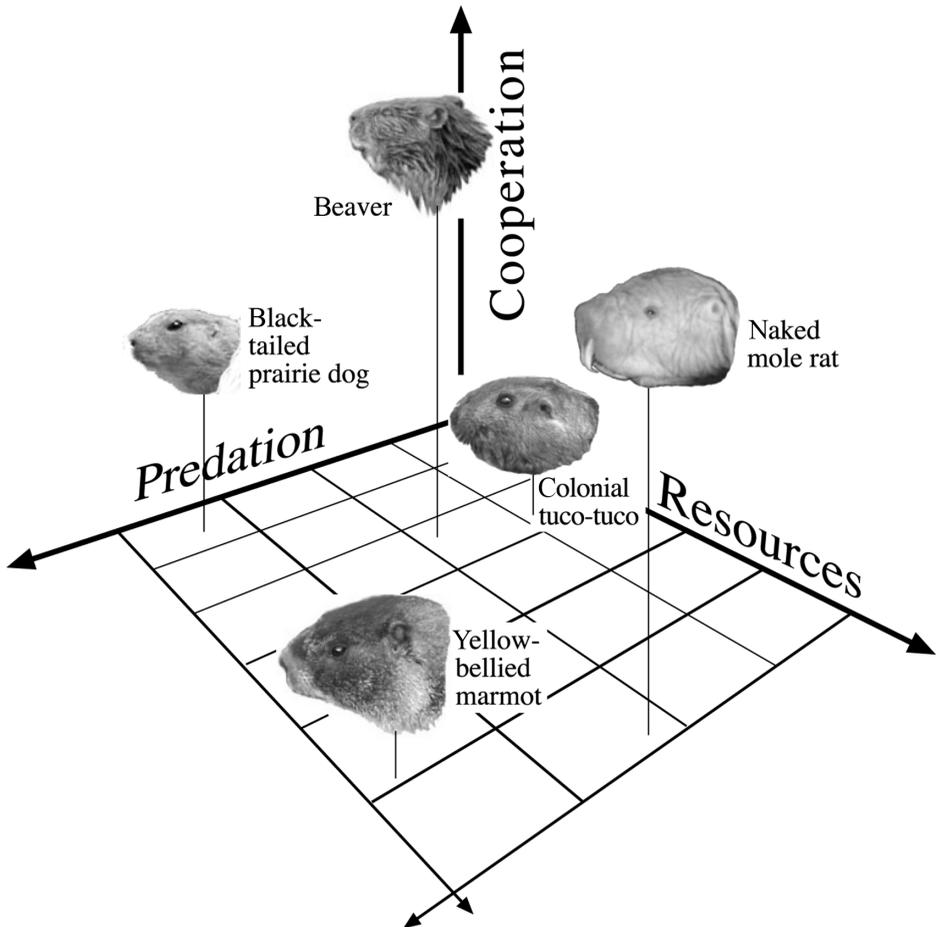


Figure 10.4 Three-dimensional conceptual model of the ecological bases for sociality. Postulated locations for several well-studied species are shown to indicate how data for these species would be represented in the model (adapted from Lacey & Sherman, 2007).

2008; Clutton-Brock & Lukas, 2012). At the other extreme, individuals may spend their entire lives in their natal group, resulting in highly kin-structured social systems, as has been suggested for naked mole-rats (Lacey & Sherman, 1997). Most species of non-primate mammals fall between these endpoints, resulting in patterns and levels of kinship vary (Smith, 2014). Although rare, the absence of kin structure within social groups has been reported for some social non-primate mammals including degus, raccoons, sperm whales, *Physeter microcephalus*, and river otters, *Lontra canadensis* (Smith, 2014). More generally, despite female philopatry, social species of bats tend to have relatively low levels of within-colony relatedness; this pattern likely reflects the presence of multiple breeding males within social groups (Burland & Worthington, 2001).

Because the majority of social non-primate mammals occur in groups containing closely related individuals of one or both sexes (e.g. Creel & Creel, 1991; Clutton-Brock, 2002;

Wilkinson & Baker, 1988; Faulkes, *et al.*, 1997), many individuals in these species interact frequently, if not primarily, with kin. This tendency is expected to significantly shape the nature of social relationships among group mates (Smith, 2014). Members of these species generally prefer to socialize with kin versus non-kin, exhibiting social preferences that parallel those in many species of primates (Chapter 9). For example, in social groups comprised of adult females that vary with regard to relatedness, females often direct more cooperative and affiliative behaviors toward their closest kin (e.g. African elephants, Archie, *et al.*, 2006; spotted hyenas, Smith, *et al.*, 2010; Indo-Pacific bottlenose dolphins, Moeller, 2012; yellow-bellied marmots, Smith, *et al.*, 2013). Interestingly, in some species, a small number of immigrant (i.e. unrelated) individuals also participate in cooperative interactions (Clutton-Brock, 2002), leading to intriguing questions regarding the interplay between direct and indirect fitness benefits in these societies. Although kin selection likely contributes substantially to the behavior of these species, future studies will benefit from expanded consideration of the range of potential adaptive benefits accruing to members of social groups characterized by variable levels of kinship.

10.7.2 Group Structure, Breeding Structure and Sex Ratio

The demographic composition, dominance structure, and social cohesion of groups have significant implications for social structure. Demographically, groups may be composed of varying ratios of males to females and may include one or multiple generations of individuals. Clearly, these elements of group structure are closely tied to the mechanisms by which groups form, notably the extent to which males and females engage in natal philopatry. Demographic structure, in turn, is critical in shaping multiple aspects of social relationships among group members, including breeding structure, dominance interactions, and the potential for cooperative care of young. Among social non-primate mammals, multi-generational groups are common, with such groups most often consisting primarily of female kin groups.

Within groups, one often conspicuous element of social structure is the presence of a dominance hierarchy. The degree to which groupmates may be ranked in a linear dominance hierarchy based on the outcomes of agonistic interactions is highly variable across non-primate mammals. For those species with pronounced dominance hierarchies, high social status often has substantial fitness benefits for carnivorans (e.g. Holekamp, *et al.*, 1996) and rodents (e.g. Huang, *et al.*, 2011), but these effects in bats, if they exist, are not well understood. Because dominance rank is often predicted by the relative age and size of individuals, the demographic structure of a group may be an important determinant of which individuals accrue such benefits. The tendency for males to have larger body sizes than females leads to the expectation that, between the sexes, males should be socially dominant over females. One striking exception occurs in spotted hyenas, in which adult females clearly dominate immigrant males (Kruuk, 1972; Frank, 1986). Female hyenas acquire social status via associative learning, also referred to as “maternal rank inheritance”; this process closely resembles rank acquisition in some Old World monkeys but appears to be unique among non-primate mammals (Engh, *et al.*, 2000; Holekamp, *et al.*, 2007).

Social cohesion among group mates, defined as the degree to which individuals within a group associate spatially and behaviorally, varies enormously among the species considered here. Group structure is spatially and temporally stable for species in which group mates are almost always together (e.g. naked mole-rats, Lacey & Sherman, 2007; African wild dogs, Creel & Creel, 1995) but is considerably more

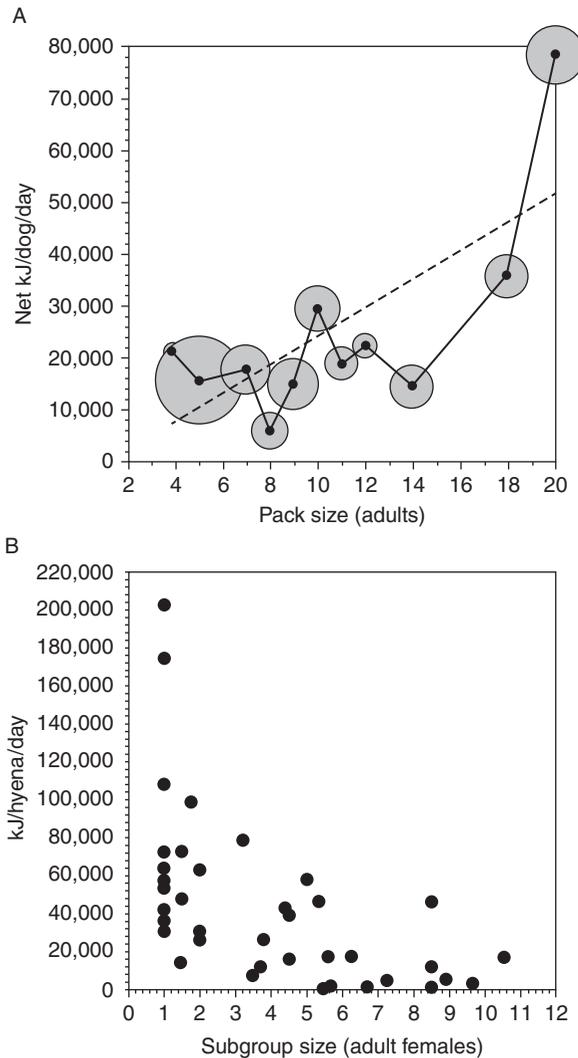


Figure 10.5 Per capita energy intake as a function of foraging group size among adult: (A) African wild dogs (reprinted from Creel, 1997) and (B) female spotted hyenas (reprinted from Smith, *et al.*, 2008). Individual points in (A) represent mean pack sizes, with sizes of surrounding gray circles proportional to the number of observations; the dashed line represents the linear regression between group size and energy intake. Points in (B) represent individual adult female hyenas observed foraging together in a subgroup after a kill has been acquired during hunting or scavenging.

fluid in species characterized by fission-fusion dynamics (e.g. spotted hyenas, Smith, *et al.*, 2008). Whereas wild dogs increase per capita energy gain from hunting in large packs, individuals within most species of social carnivorans instead often hunt alone or separate from group-mates into smaller foraging parties to reduce feeding competition at kills (Figure 10.5). Because some taxa displaying fission-fusion dynamics are often characterized by predictable, stable subgroups of individuals (e.g. elephants, Wittemyer, *et al.*, 2005), the difference in social cohesion between these and other social non-primate mammals may be more a question of scale than actual absence of cohesion. This is in apparent contrast to short-term aggregations that form around specific resources, in which no persistent relationships among group members are expected. To our knowledge, efforts to compare degrees of social cohesion beyond carnivorans (Smith, *et al.*, 2012) using a common set of metrics have not been undertaken and thus it is often unclear at what spatial and temporal levels cohesion among group mates occurs.

The sex ratio of adults in a social group tends to be closely linked to the mating system, with strongly female-biased groups often representing harem units while groups with more equitable sex ratios tend to be polygynandrous (plural breeding) or monogamous (singular breeding) (Clutton-Brock, 1988). As a result, information regarding sex ratio may generate important insights into patterns of reproductive behavior among group members. Clearly, the sex ratio of a social group is influenced by patterns of natal philopatry and group formation, with greater bias toward female philopatry expected to increase the probability of the formation of harem groups (Clutton-Brock & Iason, 1986). As a result, adult sex ratio provides an important tie between the reasons for group living and the fitness consequences to group members of living with conspecifics. The “Trivers-Willard hypothesis” (Trivers & Willard, 1973) posits that females may alter the sex ratio of young in response to differences in the costs of producing sons versus daughters and the asymmetry in breeding success of low versus high quality offspring of each sex. Although evidence for this hypothesis varies among mammals, a comprehensive meta-analysis revealed that studies focusing on female condition near the time of conception provide strong support for the prediction that mothers in good condition should bias their litters towards sons (Cameron, 2004). Given that group living may enhance the direct fitness of at least some group members, it is possible that patterns of sex ratio allocation differ between solitary and social species with otherwise similar breeding structures. Future studies that explore this theme in greater detail should generate important insights into this aspect of mammalian sociality.

Mammals exhibit a wide range of mating systems including polygyny, polyandry, polygynandry, and both social and genetic monogamy. In striking contrast to birds, less than 10 percent of mammalian species are monogamous (Lukas & Clutton-Brock, 2013), indicating that in the vast majority of the animals that are the focus of this chapter, adults of one or both sexes mate with multiple partners. Across all non-primate mammals, monogamy is particularly prevalent among elephant shrews (Macroscelidea, 14/15 or 93 percent of species), carnivorans (32/202 or 16 percent of species), and diprotodont marsupials (Diprotodontia, 2/15 or 13 percent of species). In contrast, monogamy occurs in less than 10 percent of extant species of chiropterans, rodents,

artiodactyls (even-toed ungulates), lagomorphs (rabbits, hares, pikas), and soricomorphs (shrews, Lukas & Clutton-Brock, 2013). Mating systems are known for at least 963 species of chiropterans; the vast majority live in polygynous groups with only 17 (1.8 percent) species described as monogamous (McCracken & Wilkinson, 2000). Among social mammals more generally, singular breeding is believed to have evolved from monogamy (Lukas & Clutton-Brock, 2012) and, not surprisingly, singular breeding species tend to be monogamous. Less obvious is why monogamy is generally rare among other mammals; considerable research has focused upon at identifying the ultimate and proximate bases for monogamy in the few species in which it occurs (Clutton-Brock, 1988). Given the apparent link between monogamy and singular breeding, understanding the adaptive bases for monogamy would likely generate important insights into the reasons for variation in breeding structure and correlated aspects of social structure in non-primate mammals.

III SOCIAL SYNTHESIS

Despite extensive research on a phylogenetically diverse array of species, there is still much that remains to be learned regarding the social lives of non-primate mammals. Here, we summarize what is known and outline important gaps in our understanding of the social structures of these animals, including taxa for which relevant data are particularly lacking. To conclude, we outline several ways to address these shortcomings and emphasize the need for long-term field studies (Armitage, 1991; Clutton-Brock & Sheldon, 2010), integration of proximate and ultimate information (Hofmann, *et al.*, 2014), and inclusion of new model organisms (Taborsky, *et al.*, 2015).

10.8 A Summary of Non-Primate Mammalian Sociality

Because individuals must interact to reproduce and offspring must nurse from their mothers, all species of mammals are to some degree social. However, the form and degree of sociality vary widely both within and among species. Current ecology plays a central role in this variation, influencing the tendency for groups to form, remain cohesive or to fragment. Because evolutionary history influences demographic and life history traits, phylogenetically-based analyses reveal general patterns. Given the wealth of demographic, life history, ecological, and behavioral information now available for mammals and the increasingly powerful phylogenetic tools that can be used to explore these data, the range of possible comparative studies of the evolution of social behavior in non-primate mammals is tremendous.

One critical direction for future studies of mammalian social structure is to determine the nature and magnitude of the fitness consequences associated with group living. Such analyses can yield important insights into the selective factors favoring sociality (Silk, 2007) and thus can guide efforts to link patterns of social structure to specific environmental factors, life history traits, and evolutionary parameters. For example, in species

in which group living is associated with increased per capita direct fitness (e.g. yellow-bellied marmots, Armitage & Schwartz, 2000; African wild dogs, Creel & Creel, 1995), the benefits of sociality are assumed to outweigh those associated solitary life; in species in which per capita direct fitness decreases within groups (e.g. colonial tuco-tucos, Lacey, 2004), ecological or other costs to dispersal are thought to predominate. At the same time, analyses of the fitness consequences of group living can facilitate understanding of variation in fundamental within-group social traits such as breeding structure. For example, while the relationship between per capita direct fitness and group size tends to be neutral or negative in plural breeding species, this relationship tends to be positive – at least for reproductive individuals – in singular breeding species (Ebensperger, *et al.*, 2012). Collectively, these contrasts suggest that further comparative analyses of patterns of direct fitness will yield critical insights into the causes and consequences of sociality in non-primate mammals.

The majority of information summarized here comes from studies of a relatively limited number of carnivorans and rodents, with information from social chiropterans being particularly underrepresented. Long-term field studies conducted in natural settings are essential for linking patterns of behavior to the selective environments in which they occur, as has been attempted for carnivorans (Smith, *et al.*, in press), rodents (Hayes, *et al.*, in press), and bats (Kerth & Van Schaik, 2012). Equally importantly, long-term studies can reveal significant patterns of variation that are not evident over short time scales (Clutton-Brock & Sheldon, 2010), such as the lifetime fitness trajectories of individual dwarf mongooses (Creel & Waser, 1994), the impact of inter-annual environmental variation on reproductive success among female degus (Ebensperger, *et al.*, 2014), the social and fitness consequences of subordinate breeding in meerkats (Young, *et al.*, 2006), the lifetime impacts of inherited social rank in spotted hyenas (Holekamp, *et al.*, 2012), and the implications of decadal patterns of environmental change on the demography and behavior of yellow-bellied marmots (Blumstein, 2013). In addition to increasing the number and diversity of mammalian taxa for which information is available, we advocate the collection of behavioral, demographic, and ecological data across multiple generations of free-living individuals to allow for greater understanding of relationships among environmental conditions, adaptive consequences, and patterns of social structure.

10.9 Comparative Perspectives on Non-Primate Mammalian Sociality

This review identifies emergent patterns of mammalian social structure. Expanding the scope of these comparisons to include primates as well as members of other animal lineages reveals intriguing similarities and differences in social behavior. Species considered here are similar to primates in that cognitive abilities appear to play an important role in shaping patterns of nepotism and communication. Social dominance hierarchies and fission-fusion dynamics within many of the social non-primate mammals resemble those of primates. With regard to other vertebrates, group defense and predator detection reviewed here mirror those of some birds and fish. Patterns of

dispersal and parental care are in direct contrast to predominant patterns for birds (Chapter 11). More generally, some mammals cooperate to acquire resources and to rear young. As in most other vertebrates, but in striking contrast to the caste structure found in many insect societies, non-primate mammals apparently lack morphological and physiological specializations for reproductive division of labor. This raises intriguing questions about the ecological and evolutionary bases for this apparent difference between social vertebrates and invertebrates. It also raises important questions regarding the differences within vertebrates that have led to remarkable parallels between social insects and a very limited number of (eu)social rodents. In sum, we expect that future broad-scale comparative studies that explore these types of similarities and differences in greater detail will prove highly informative regarding the ecological and evolutionary bases for variation in animal social structure.

10.10 Concluding Remarks

The study of mammalian social behavior has reached an exciting juncture due to emerging opportunities to integrate extensive data sets from long-term field studies with rapidly expanding molecular and neurobiological technologies capable of revealing the proximate substrates for social interactions (Blumstein, *et al.*, 2010; Hofmann, *et al.*, 2014). In the decades since the publication of Eisenberg's (1966) seminal review of the social behavior of mammals, multiple long-term (and often ongoing) studies of social structure have been initiated for free-living populations of carnivorans, rodents, and bats (e.g., Kerth & Van Schaik, 2012; Hayes, *et al.*, in press; Smith, *et al.*, in press). These efforts continue to reveal new and intriguing relationships among social behavior, ecology, demography, and life history traits. To capitalize upon these efforts and to better delineate the role of evolutionary history in shaping such relationships, the taxonomic coverage of field research programs needs to be expanded, with particular attention to studies of social chiropterans. At the same time, the ever-changing technological landscape is improving our ability to examine physiological and genetic mechanisms of social behavior in free-living animals and these emerging opportunities promise to yield important new insights into variation in social structure.

We hope that the overview of non-primate mammalian social structure provided here – including the gaps in understanding and taxonomic coverage that we have highlighted – will serve to stimulate considerable additional research on all aspects of the social behavior of these fascinating animals. As field biologists, we strongly encourage efforts to characterize patterns of behavior as they occur in natural selective environments. As active participants in collaborative studies of neurobiological, endocrine and genetic underpinnings for social behavior, we advocate integrative efforts to understand variation in social structure. Ideally, readers of this chapter – including both established scientists and future experts in behavior – will be intrigued by the emergent trends in mammalian sociality that we have described and will build upon this foundation to undertake new and exciting studies of social structure in this important clade.

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