Chapter 12
Cooperation and Conflict in the Social Lives of Bats

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Abstract To be evolutionarily stable, cooperative behavior must increase the actor's lifetime direct fitness (mutualism) or indirect fitness (altruism), even in the presence of exploitative, noncooperative "cheaters." Cooperators can control the spread of cheaters by targeting aid to certain categories of individual, such as genetic relatives or long-term social partners. Without such discrimination, cheaters could gain the reproductive benefits of cooperation without paying the same costs and eventually outbreed cooperative phenotypes. Here, we review evidence for cooperative behaviors in bats and the possible mechanisms that might prevent cheating. Cooperative behavior in bats is shaped by ecology, life history, and social structure. Altruism without kin discrimination is unlikely to evolve through population viscosity in bats because dispersal leads to low-average relatedness in the colony or social group. On the other hand, mutually beneficial cooperation, often between unrelated individuals, is found in several bat species. Examples include social thermoregulation, male cooperation for defense of female groups, female cooperation for defense of food and pups, social grooming, and food sharing. Many forms of cooperation in bats likely involve both direct and indirect fitness benefits. Some group-living tropical bat species provide intriguing examples of costly helping behavior between unrelated individuals, but the exact mechanisms that prevent cheating remain to be tested.

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R.A. Adams and S.C. Pedersen (eds.), *Bat Evolution, Ecology, and Conservation*,
DOI 10.1007/978-1-4614-7397-8_12,

12.1 Introduction

Natural selection favors various forms of cooperation at every level of life from genes to cells to individuals to social groups. Cooperative behaviors increase the fitness of recipients and are adaptive because they promote the actor's own direct fitness, increase indirect fitness by helping a genetic relative (kin selection), or some combination of both (Table 12.1). All forms of social life from microbial biofilms to insect and human societies involve mechanisms that maintain cooperation and suppress conflict. Without these mechanisms, helping behaviors or public goods would be exploited by noncooperative "cheaters" that can gain the reproductive benefits without paying the costs. Here, we describe evidence for cooperative behaviors in bats and discuss what behaviors might prevent cheating. Before discussing specific examples, we briefly review the underlying social evolution theory. Further review of social evolution is provided by West et al. (2007a), Wenseleers et al. (2010), and Bourke (2011).

12.2 Inclusive Fitness Theory

Hamilton (1964) solved the long-standing puzzle of why natural selection sometimes rewards organisms that sacrifice their own lifetime reproductive success to help others. Within evolutionary constraints, organisms should evolve to maximize a quantity he called inclusive fitness, which includes the transmission of genes via both personal reproduction (direct fitness) and by helping genetic relatives reproduce (indirect fitness). Hamilton's concept of inclusive fitness updated the original concept of fitness based on offspring production: adaptations evolve because they increase inclusive fitness, not just offspring production. Thinking of individual organisms as "inclusive fitness maximizers" has provided among the most testable and successful hypotheses in social behavior (Davies et al. 2012). Hamilton showed that altruism evolves when the reproductive benefits to others (B), scaled by the coefficient of relatedness (r), exceed the reproductive costs to the helper (C), i.e., $rB > C$, an inequality now known as Hamilton's rule.

To distinguish inclusive fitness theory from early, flawed theories of group selection, paths to cooperation via indirect fitness benefits were confusingly termed "kin selection" by Maynard-Smith (1964), despite kin selection not really being a form

Table 12.1 Categories of adaptive social behavior

Effect on actor's direct fitness	Effect on recipient's direct fitness	
	Increase	Decrease
Increase	Mutualism or mutual benefit	Selfishness or parasitism
Decrease	Altruism	Spite
	Cooperation	**Conflict**

Adapted from Hamilton (1964) and West et al. (2007b). Effects on direct fitness are measured in average lifetime offspring production. Altruism and spite are maintained solely by indirect fitness (kin selection) of selection and not requiring shared familial ancestry as would be observed in a pedigree (e.g., "greenbeards," Hamilton 1964; West and Gardner 2010). Kin selection does not even require kin recognition, because it can occur passively via limited dispersal. Yet, the term "kin selection" still leads to the common semantic misunderstanding that kin selection and modern forms of group selection (i.e., multilevel selection) are alternative competing hypotheses, rather than alternative ways of modeling the same biological process (e.g., Wade et al. 2010). Inclusive fitness models can implicitly account for the effects of competition between groups even when those groups are not explicit in the model, just as multilevel selection models can implicitly capture the effects of relatedness even when relatedness is not explicit in the model. In this way, the two approaches are mathematically equivalent (Wenseleers et al. 2010; Bourke 2011), as both models can involve the same nonrandom association of cooperative genotypes.

Although originally developed to explain altruism in insect societies, social evolution theory is now routinely applied to fields as diverse as microbiology, medicine, agriculture, and the social sciences (e.g., Denison et al. 2003; Foster 2005; Kümmerli et al. 2009). The diversity of applications reflects the central role of cooperation at every level of life, wherever reproducing entities cooperate in groups: genes within genomes, genomes within cells, cells within organisms, organisms within groups, and members of different species in interspecific mutualisms. At all these levels, cooperation is potentially vulnerable to exploitative "cheating" that occurs when individuals benefit from defecting from cooperation. Examples of cheating include genes that transmit themselves at the expense of the rest of the genome, cancer cells that replicate at the expense of the individual, social group members that receive aid but do not help others, eusocial insect workers that lay their own eggs rather than only tending the eggs of the queen, or flowers attracting pollinators without providing a nectar reward. Social evolution can often be seen as a coevolutionary arms race between cooperative and cheating strategies.

Inclusive fitness theory explains why cooperation evolves, but does not specify the mechanisms that maintained or enforce it. The benefits of receiving help (B) and costs of giving help (C) in Hamilton's rule are determined by the social and ecological circumstances individuals typically encounter in their natural environment and are often frequency dependent since they may be influenced by the conditional behavior of social partners. Moreover, the relative importance of direct and indirect benefits and the particular mechanisms that prevent cheating are still open questions across a wide range of organisms, including bats. To estimate the fitness costs and benefits of social behaviors in bats, it is crucial to know about both kinship and social structure.

12.3 Kinship and Social Structure in Bats

The social and mating systems of the roughly 1,260 species of Chiroptera have greatly diversified over the last 50 million years. Bats are primarily tropical (~75 % of species) and follow the general mammalian social pattern: females aggregate around important resources—including food, roosts, or conspecifics—whereas males compete for access to females (Clutton-Brock 1989). Although most tropical bats are polygynous, overall bats display a diverse spectrum of mating systems, ranging from social monogamy to promiscuity. McCracken and Wilkinson (2000) categorized 66 species (~5 %) into mating systems based on seasonality, sex composition of groups, and whether mating occurs within or outside roosts. More recent reviews of social and mating systems include Wilkinson (2003), Zubaid et al. (2006), and Kerth (2008a).

Limited dispersal, including natal philopatry, can result in high relatedness among social group members and thus has important implications for social evolution. Kin selection via limited dispersal occurs when individuals cooperate indiscriminately with neighboring individuals that are genetically related on average (Hamilton 1964). However, evidence suggests that conditions of high-average relatedness within groups or colonies are rare or absent in most bats.

Natal philopatry can lead to competition among kin that reduces or completely negates the indirect fitness benefits of helping relatives (Hamilton and May 1977; West et al. 2002). In other words, the easiest way to benefit kin might be to disperse and avoid competing with them (Hamilton and May 1977; Kümmerli et al. 2009). Kin competition can be reduced in theory if subsets of relatives leave the natal colony as a group (i.e., budding dispersal, Gardner and West 2006; Kümmerli et al. 2009), and interestingly, this pattern has been found in at least one bat species (*Eptesicus fuscus*, Metheny et al. 2008a; Kerth 2008b).

Natal philopatry of both sexes can lead to inbreeding. In bats, the typical pattern is female philopatry and male dispersal resulting in social groups with matrilineal kin, where immigration and visitation by foreign males reduce average group relatedness and inbreeding (e.g., Wilkinson 1985; Kerth and Morf 2004). In species where dominant males typically remain resident longer than the age of female sexual maturity, females tend to disperse to avoid mating with their fathers (*Lophostoma silvicolum*, Dechmann et al. 2007; *Saccopteryx bilineata*, Nagy et al. 2007; *Rhynchonycteris naso*, Nagy et al. 2013; other mammals, Lukas and Clutton-Brock 2011). The same conditions probably explain the complete female dispersal found in *Phyllostomus hastatus* (McCracken and Bradbury 1981) and female movements between different social groups in *Artibeus jamaicensis* (Morrison and Handley 1991).

Average colony relatedness in bats remains low even when pairwise relatedness values between certain individuals are high. For example, *Myotis bechsteinii* live in closed female groups with 75 % of females roosting with close relatives ($r = 0.25$ or greater), yet mean colony relatedness is still quite low ($r = 0.02$, Kerth et al. 2002). Similar patterns are found in other species (e.g., Wilkinson 1985; Burland et al. 2001; Metheny et al. 2008b; Boston et al. 2012; Patriquin et al. 2013). Even unusually high levels of pairwise relatedness do not translate to high-average colony relatedness. For example, in *Rhinolophus ferrumequinum*, some females mate with the same male across years and other females mate preferentially with the same male as their mother. As a consequence, pairwise relatedness between resulting progeny is elevated two to five times above normal (Rossiter et al. 2005). Yet, mean colony relatedness remains low ($r = 0.03$, Rossiter et al. 2006).

In social species where pairwise relatedness is on average low within groups but highly variable among pairs, as is the case in most bats, individuals are expected to actively discriminate kin rather than rely on indiscriminate altruism and limited dispersal (Cornwallis et al. 2009). Kin discrimination based on phenotypic matching of olfactory or vocal cues would benefit individuals whenever kin and non-kin intermingle. For example, in the group-living *Desmodus rotundus* where individuals are surrounded by non-kin (average, $r = 0.02–0.11$), females groom and regurgitate food with close relatives more than expected by chance (Wilkinson 1984, 1986). Similarly, average relatedness with roostmates is low in *Myotis septentrionalis*, but related pairs were more likely to associate and switch roosts together than unrelated pairs (Patriquin et al. 2013). Unlike cooperatively breeding birds and mammals, bats rarely, if ever, live in extended family groups; therefore, helping behaviors in bats that are directed indiscriminately within groups are likely mutually beneficial rather than altruistic.

Patterns of mating, dispersal, and survival determine kinship structure, but except for maternal care, kinship is not always a strong determinant of cooperation in bats. Non-kin cooperation is found in several species (e.g., *D. rotundus*, Wilkinson 1984; *M. bechsteinii*, Kerth et al. 2011; *P. hastatus*, Wilkinson and Boughman 1998; Bohn et al. 2009), and, on the other hand, highly related female *R. ferrumequinum* do not demonstrate obvious strong cooperative behaviors (Rossiter et al. 2002, 2006). Ecological factors, which determine costs and benefits of cooperation, are likely to shape the occurrence of cooperative behaviors in bats.

12.4 Cooperation and Conflict as a Coevolutionary Arms Race

For some cases of cooperation, there appears to be no cost to cooperating and hence no potential for cheating (by-product mutualisms). Consider, for instance, bats making drinking passes at watering holes from a single direction to avoid collisions (Adams and Simmons 2002). However, once a by-product benefit is established, investments in a mutualism may evolve that yield higher returns (Connor 1986). For example, in species where young cluster together in crèches (Fig. 12.1a), females

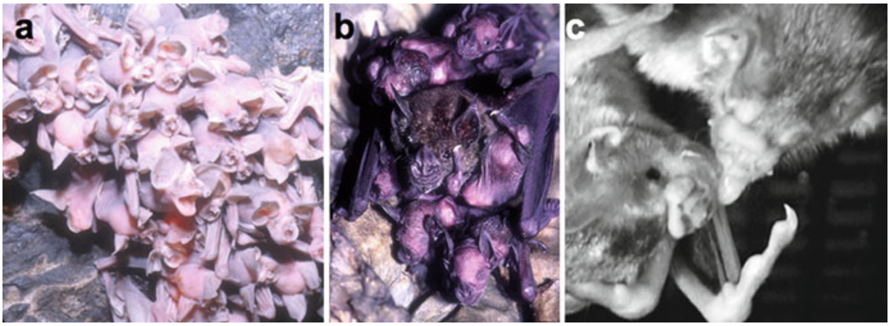

Fig. 12.1 Examples of cooperative behavior in bats. (**a**) Pups like these *Rhinolophus darlingi* may mutually benefit from clustering together for warmth. (**b**) A female *Phyllostomus hastatus* roosting with several non-offspring pups in Trinidad. (**c**) Regurgitated food sharing between unrelated adult *Desmodus rotundus*

might benefit from helping non-offspring pups survive if their own pups gain thermoregulatory benefits with larger crèche sizes (an example of a hypothesis called "group augmentation," Kokko et al. 2001). Besides thermoregulation, bats may associate for the direct benefits of avoiding predators (*Pteropus poliocephalus*, Klose et al. 2009) or learning about roosts and feeding sites (e.g., Wilkinson 1992b, 1995; Kerth and Reckardt 2003; Ratcliffe and Hofstede 2005; Safi and Kerth 2007; Dechmann et al. 2009, 2010). The significance of social information on the evolution of sociality is suggested by the finding that male sociality in temperate bats evolved more often in lineages that forage on ephemeral insects in open habitats—conditions where eavesdropping is most likely (Safi and Kerth 2007).

Opportunities to cheat can be subtle. For instance, huddling for thermal benefits (e.g., Pretzlaff et al. 2010) is often regarded as a by-product mutualism that does not require enforcement; yet, cheating is possible if an individual can maintain a lower body temperature than its neighbors, saving energy while still being kept warm by others ("the huddler's dilemma," Haig 2008). Similarly, social information about food can lead to frequency-dependent selection between "producer" strategies that invest in finding food and "scrounger" strategies that instead follow others (Barnard and Sibly 1981). For example, aerial-hawking bats might eavesdrop on hunting conspecifics and steal their prey (Chiu et al. 2010) or vampire bats might drink from wounds opened by other individuals (GGC and GSW, personal observations).

To prevent exploitative strategies from invading, cheating prevention is required. Kin discrimination can prevent cheating by ensuring that helpers aid primarily genetic relatives. Individuals can enforce non-kin cooperation through various forms of conditional reward or punishment. Such enforcement might involve individuals actively punishing cheaters, decreasing cooperative investments, or switching away from social partners that cheat (Trivers 1971; Noë and Hammerstein 1994; West et al. 2007a; Fruteau et al. 2011) and are described by many terms in the literature including reciprocal altruism, reciprocity, sanctions, rewards, partner control, or partner choice (West et al. 2007b; Bshary and Bronstein 2011).

Such mechanisms of enforcement are necessary to explain the persistence of cooperative behaviors that pose energetic costs with potential negative fitness consequences (Table 12.2). Below, we describe evidence for such helping behaviors in bats. We illustrate how altruistic parental care is exploited by foreign pups, how conditions of intense competition between unrelated males can select for alliances between related males, how competition between groups for food might select for cooperative foraging within groups, how infanticide can lead to pup guarding, and how the need to enforce cooperation might lead to partner fidelity and long-term social bonds.

12.5 Cooperative Behaviors in Bats

12.5.1 Alloparental Care

There are many anecdotal observations of bats nursing non-offspring pups in the wild (*Tadarida brasiliensis*, *Nycticeius humeralis*, *Pipistrellus pipistrellus*, *Miniopterus schreibersi*, *P. hastatus*) or in captivity (*Eidolon helvum*, *Rousettus*

Table 12.2 Cooperative behaviors in bats that pose costs to the helper

Behavior	Key references	What might prevent cheating?
Alloparental nursing	McCracken and Gustin (1991), Wilkinson (1992a)	1. Kin discrimination: help is targeted to genetic relatives 2. By-product mutualism: cheating is impossible if alloparental nursing leads to higher milk yield, increased milk fat, or reduced mastitis 3. Group augmentation: increases in colony size benefit mother or offspring by increasing social information
Food sharing	Wilkinson (1984), Carter and Wilkinson (2013)	1. Kin discrimination 2. Reciprocity: bats share with reciprocators and withhold sharing with non-reciprocating cheaters
Social grooming	Wilkinson (1986), Kerth et al. (2003), Kerth (2008a), Ancillotto et al. (2012), Carter and Wilkinson (2013)	1. Kin discrimination 2. Reciprocity 3. Exchange: bats reciprocate social grooming for other services within a long-term social bond
Cooperative mate guarding	Ortega et al. (2008), Nagy et al. (2012)	1. Kin discrimination 2. Helpers more likely to inherit dominant status
Pup guarding	Bohn et al. (2009)	1. Group augmentation 2. Exchange

aegyptiacus, *Macrotus californicus*, *P. pipistrellus*, *T. brasiliensis*, *D. rotundus*, *Diaemus youngi*), as well as some observations of conspecifics helping with birth (*Pteropus rodricensis*) or adopting pups in captivity (*D. rotundus*, *Diphylla ecaudata*, *Cynopterus brachyotis*, Kunz et al. 1994, LeBlanc 2001, and refs therein, Delpietro and Russo 2002). However, in most cases, it is unknown if such helping behaviors are evolved adaptations or simply by-products of maternal care.

Prior to inclusive fitness theory, such behaviors were thought to occur for the good of the colony or species. For example, nursing female *T. brasiliensis* were thought to "act as one large dairy herd delivering milk passively…to keep the milk supply distributed among the caves in proportion to demands for it" (Davis et al. 1962). Wild female *T. brasiliensis* nurse pups that are not their own offspring in at least 17 % of observed cases (McCracken 1984), but this behavior is best understood as successful milk parasitism by unrelated pups. Given the chance, *T. brasiliensis* pups will attempt to nurse from non-mothers that respond by hitting, scratching, and biting them (McCracken and Gustin 1991).

Milk parasitism likely occurs in other species as well. *S. bilineata* pups respond to non-maternal female calls (Knörnschild and von Helversen 2008), and *N. humeralis* pups attempt to nurse from non-maternal females with increasing frequency starting at 8 days of age (Wilkinson 1992a). During two summers of observation of *N. humeralis*, females almost always allowed nursing by offspring, but rejected at least 23 % of attempts by non-offspring pups by covering their nipple, moving away, or biting at persistent pups (Wilkinson 1992a).

Yet, *N. humeralis* mothers also nursed offspring that were not their own in at least 20 % of nursing bouts, and two hypotheses can explain how alloparental nursing might be adaptive for nursing females. First, alloparental nursing might be explained as "milk dumping" to decrease weight and improve foraging ability. As in other mammals, incomplete suckling might decrease milk yield, decrease percentage of fat in milk, and increase rate of mastitis. Also, the peak of alloparental nursing coincided with the annual peak in prey density, when mothers would be predicted to have excess milk (Wilkinson 1992a). This by-product mutualism hypothesis predicts that alloparental nursing would correlate with higher post-foraging mass gain.

A second group augmentation hypothesis is that alloparental nursing increases colony size, and subsequently, social information available to mother and offspring (Wilkinson 1992a, b). *N. humeralis* preferentially nursed non-offspring pups that were female and hence philopatric, even those mothers with male offspring. This hypothesis predicts that groups with more female pups should yield greater pup survival.

12.5.2 Cooperative Male Defense of Females

In bats, there are no known cases of cooperative breeding, where subordinates help a dominant female breed. However, there is evidence of male bats forming cooperative alliances to monopolize females, similar to the male alliances found in dolphins (Connor et al. 1992) and chimpanzees (Watts 1998). In polygynous species, dominant males often tolerate the presence of other less dominant males, especially relatives, and these subordinate males often appear to help ward off foreign males (Ortega et al. 2003). In *A. jamaicensis*, dominant males lose paternity to both subordinates and visiting foreign males, but dominants are able to defend larger female groups with the help of subordinates, and also benefit indirectly if subordinates that sire offspring are related. In return, subordinate males gain greater access to females, increased chances to acquire dominant status, and indirect benefits if they are related to dominants (Ortega et al. 2003, 2008). Such alliances between dominants and subordinates can last more than 2 years (Ortega et al. 2008). In *S. bilineata*, dominant males benefit from subordinate males that queue for dominant status (Voigt and Streich 2003; Nagy et al. 2012). In this species, dominant male tenure duration is not correlated with number of females or forearm size (a proxy of body size), but tenure duration does increase with the number of subordinate males on their territory (Nagy et al. 2012).

12.5.3 Cooperative Female Defense of Food and Pups

Whereas access to females is the key limit on male fitness, access to food and roosts is the equivalent limitation on female fitness. Not surprisingly then, there is also evidence that females cooperatively monopolize and defend food resources from other females. Female greater spear-nosed bats, *P. hastatus*, live and cooperate with unrelated groupmates. Since both sexes disperse from their natal group, the 10–22 adults in a group are unrelated (McCracken and Bradbury 1981). On the island of Trinidad, between 4 and 40 groups coinhabit various caves, each group located in a ceiling alcove guarded by a resident male. Female groupmates give birth synchronously (Porter and Wilkinson 2001) and cooperatively forage and defend food patches such as large fruiting trees (Wilkinson and Boughman 1998). Group members coordinate their movements using socially acquired, group-specific "screech calls" that convey group membership but not individual identity (Boughman 1998; Boughman and Wilkinson 1998). These calls also appear to facilitate cooperative mobbing of predators (Knörnschild and Tschapka 2012). In contrast, pups produce individually distinct "isolation calls" (Bohn et al. 2007).

Isolation calls allow mothers to find, recognize, and retrieve their pups that have fallen to the ground (Bohn et al. 2007, 2009). Falls are surprisingly common; Bohn et al. (2009) observed 85 pups (~4 % of all non-volant pups) fall to the cave floor during 50 h of observation. And these fallen pups will die quickly if not retrieved. In one cave, 17 females visited and inspected fallen pups as many as 342 times (Bohn et al. 2009). Mothers will retrieve their pups, but females from other groups will often bite pups, and sometimes carry away and kill them. Females from the same social group, on the other hand, while not retrieving the pup themselves, will often guard pups from attacking non-groupmate females (Bohn et al. 2009). Males ignore fallen pups.

Female *P. hastatus* appear to cooperate with unrelated groupmates and compete with non-groupmates. But given that all offspring disperse, what do adult females gain from the survival of pups in their social group? One possibility is group augmentation (Kokko et al. 2001): that females guard pups to ensure that warm bodies surround their own pup when they are out of the cave foraging. This hypothesis predicts that pup guarding increases or helps maintain pup numbers in the group towards an optimum (Kokko et al. 2001) and is consistent with the unusual synchrony of births within groups (Porter and Wilkinson 2001; Bohn et al. 2009). Yet, data on group size and pup fitness show either no effect (Boughman 2006) or a negative linear correlation between group size and pup condition (Bohn et al. 2009). However, an optimal group size might produce a unimodal, rather than linear, relationship between group size and pup survival. Furthermore, long-term field studies of cooperatively breeding birds and mammals show that the effects of cooperation on the fitness of young can be subtle and slow acting; hence lifetime fitness benefits cannot be discounted even when no short-term benefits are obvious (Hatchwell et al. 2004; Russell et al. 2007; Brouwer et al. 2012). More data are therefore needed to determine the relationship between lifetime reproductive success and group size in *P. hastatus* and other bats.

A second possibility is that females somehow enforce the direct fitness benefits of pup guarding. Bohn et al. (2009) found no evidence for direct reciprocity, that mothers guard pups to enforce guarding of their own pup. There was no correlation between guarding pups and having one's own pup guarded, or between time guarding and time having one's own pup guarded (Bohn et al. 2009). It is possible that females "exchange" pup guarding for other cooperative services, such as some of the behaviors described above or the possibility of "babysitting" when adults stay behind with several pups (GSW personal observation, Fig. 12.1b), but documentation of such exchanges, or exclusion of less cooperative individuals, remains to be obtained.

12.5.4 Food Sharing

When adult female or young *D. rotundus* miss a nightly meal, female roostmates will typically regurgitate some of their own blood meal to feed them (Wilkinson 1984). Female donors regurgitated blood mostly for their own offspring (70 % of cases) but also for other hungry adult females (Fig. 12.1c). Adult food sharing correlates independently with both relatedness and roosting association (Wilkinson 1984). Reciprocal food sharing in *D. rotundus* is frequently cited as an example of reciprocity, but it also demonstrates kin discrimination because more than 95 % of food sharing occurred between close relatives ($r < 0.25$) despite the majority of possible donors being unrelated (Wilkinson 1984). On the other hand, simulations demonstrate that, if reciprocity exists, the resulting direct fitness benefits would greatly exceed the indirect fitness benefits (Wilkinson 1988). Hence, it is possible that *D. rotundus* base their helping decisions on past social experience rather than cues to relatedness. Others have proposed that food sharing between non-kin only occurs due to kin recognition errors (Hammerstein 2003), harassment of potential donors (Clutton-Brock 2009), or group augmentation (Davies et al. 2012).

To test these alternative hypotheses, we induced food sharing in *D. rotundus* under controlled captive conditions of varying relatedness and equal roosting association (Carter and Wilkinson 2013). We found that the majority of donations were initiated by donors and hence could not be explained by harassment. The dyadic patterns of food sharing were reciprocal, correlated with grooming, and stable over time. Reciprocal donations were eight times more important than pairwise relatedness estimates for predicting food donations under conditions of equal association (Carter and Wilkinson 2013).

A multilevel selection model (Foster 2004) assumes that donors do not discriminate between unfed bats when giving blood and suggests that food sharing could in theory evolve without kin discrimination or reciprocity. However, this model ignores several important factors: the possibility of cheating, the frequent roost switching and fluid fission–fusion dynamics that make *D. rotundus* social groups unstable in membership (Wilkinson 1985), and the evidence that food is not shared indiscriminately among group members (Wilkinson 1984; Carter and Wilkinson 2013).

Reciprocity can exist in *D. rotundus* assuming they remember past social experiences and invest accordingly, which is consistent with this species possessing the largest brain and neocortex relative to their body size among bats (Baron et al. 1996). To demonstrate reciprocity, however, one must show that the bats will punish cheaters by switching partners or decreasing investment to those partners who provide poor returns.

Regurgitated food sharing is found in all three vampire bat species (Wilkinson 1984; Elizalde-Arellano et al. 2007; Carter et al. 2008), but has not been found in other bats. Work on primates suggests that the evolution of adult food sharing is predicted by several factors: the difficulty of obtaining and processing the diet, parental feeding of young, and opportunities for partner choice in other contexts, such as mating or other mutualisms (Jaeggi and van Schaik 2011). Whereas some of these conditions do occur in some other bat species (e.g., parental food sharing from cheek pouches in *Noctilio albiventris*, Brown et al. 1983, or transfer of a captured prey from adult to young in some carnivorous bats, *Megaderma lyra*, Raghuram and Marimuthu 2007; *Vampyrum spectrum*, GSW personal observation), *D. rotundus* satisfy all the conditions.

12.5.5 Social Grooming

Mothers routinely groom their pups (e.g., McLean and Speakman 1997), but social grooming also occurs between adult bats in some species (*D. rotundus*, *D. youngi*, *D. ecaudata*, *A. jamaicensis*, *P. hastatus*, *M. bechsteinii*, and *Pipistrellus kuhlii*, Wilkinson 1986; Kerth 2008a; Ancillotto et al. 2012, GSW and GGC personal observation). In some cases, social grooming appears nepotistic and explained by kin selection. Kerth et al. (2003b) found that social grooming between adult female *M. bechsteinii* was not significantly reciprocal but was correlated with kinship, occurring mostly between adult mothers and daughters, sometimes between sisters, and rarely between non-kin. Kin-biased social grooming also occurs in female *D. rotundus* (Wilkinson 1986).

In primates, social grooming provides a social purpose beyond its hygienic function and has become co-opted over evolutionary time as an important signal of social investment. A similar process may have occurred in some bat species. Consistent with this hypothesis, patterns of social grooming do not correlate with patterns of self-grooming or amounts of parasites (Wilkinson 1986; Kerth et al. 2003), and reciprocal social grooming remains common among captive-born *D. rotundus* that completely lack observable external parasites (Carter and Wilkinson 2013). Although *D. rotundus* groom themselves less than *M. bechsteinii*, female *D. rotundus* groom their roostmates about twice as often as female *M. bechsteinii* (Wilkinson 1986; Kerth et al. 2003). When controlling for kinship, social grooming among female *D. rotundus* is predicted by roosting association and food sharing and is elevated immediately prior to food sharing (Wilkinson 1986). When mother-offspring pairs are excluded, the effect of roosting association and food sharing on mutual grooming exceeds that of relatedness (Wilkinson 1986; Carter and Wilkinson 2013).

The correlation between social grooming and food sharing in *D. rotundus* highlights the possibility that cooperative behaviors can lead to cooperative social bonds (Carter and Wilkinson 2013). For example, one scenario for the evolution of cooperation in vampire bats is that regurgitated food sharing evolved initially as part of maternal care and was then co-opted as a form of altruism towards other close relatives. Natural selection would reward individuals that preferentially fed those relatives that were not only more related but also more likely to reciprocate. Smaller investments, such as social grooming between adults, could then act as costly signals for larger social investments (e.g., Roberts and Sherratt 1998; Fruteau et al. 2011) such as food sharing. Since partner fidelity makes cooperative investments less risky, the continuation of investments should promote long-term social bonds and vice versa.

12.6 Social Bonds and Complex Cooperation

The ages of females in social groups suggest that similarly aged cohorts form roosting associations in many bats (e.g., McCracken and Bradbury 1981; Wilkinson 1992a; Brooke 1997; Porter and Wilkinson 2001), but little is known about the development and formation of social relationships among individuals. When *P. kuhlii* pups were raised together for 6 weeks in separate groups and then allowed to freely interact in a flight chamber, young raised in the same groups showed significantly higher rates of clustering, social grooming, and roosting near each other (Ancillotto et al. 2012).

Once associations are formed, they might be maintained by eavesdropping on echolocation calls (e.g., Jones and Siemers 2011; Schuchmann and Siemers 2010; Voigt-Heucke et al. 2010), but this is limited by call amplitude (Hoffmann et al. 2007; Ruczyński et al. 2009). Social calls are lower in frequency, more variable, and travel farther distances. Contact calls allow isolated individuals to find and identify roostmates at a distance (*D. youngi*, Carter et al. 2008, 2009; *D. rotundus*, *D. ecaudata*, Carter et al. 2012; *Thyroptera tricolor*, Chaverri et al. 2010; Gillam and Chaverri 2011; *M. bechsteinii*, *M. nattereri*, Schoner et al. 2010; *Antrozous pallidus*, Arnold and Wilkinson 2011; *Nyctalus noctula*, Furmankiewicz et al. 2011) and may also carry information about genetic relatedness (*A. pallidus*, Arnold 2011) or group affiliation (*P. hastatus*, Boughman and Wilkinson 1998). At closer range, recognition, and perhaps bonding, is likely mediated through social grooming or mutual scent marking (*D. rotundus*, Wilkinson 1986; *N. leporinus*, Brooke 1997; *M. bechsteinii*, Safi and Kerth 2003; *D. youngi*, GGC personal observation).

Females are known to form long-term associations in both tropical and temperate bat species. For example, unrelated pairs of female *P. hastatus* have been recorded roosting together 16 years later (Wilkinson and Boughman 1998), and pairs of female *D. rotundus* have been found together after 12 years (Wilkinson 1985). *M. bechsteinii* is a temperate species that maintains social bonds that last over 5 years and span categories of age, size, reproductive status, and kinship (Kerth et al. 2011). *M. septentrionalis* form significant associations for at least 3 years (Patriquin et al. 2010). In both species, relationships persist despite frequent roost switching and annual disintegration of group structure during winter. Given that bats are unusually long-lived for their size (Wilkinson and South 2002), we suspect that long-term social bonds occur in many other bat species.

There are several good reasons to maintain long-term rather than short-term mutually beneficial social relationships. Partner fidelity reduces the cost of searching for and learning about partners, allows one to invest gradually in cooperation to limit losses from cheating, and bundles the benefits from multiple forms of cooperation into a single relationship. For example, affiliated female *D. rotundus* might in effect exchange and monitor multiple forms of social investment including social thermoregulation, social grooming, information transfer, and food sharing. According to this hypothesis, social bonds permit fitness benefits to be mutually exchanged and enforced. This hypothesis predicts that change of a social bond by increase or decrease of one cooperative behavior will lead to the same change in other cooperative behaviors by the social partner. Furthermore, a decrease in one's capacity to perform a helping behavior (e.g., food sharing) could lead to an increase in other cooperative behaviors (e.g., grooming) to compensate and maintain the social relationship.

12.7 Future Avenues of Research

Many important questions remain regarding social evolution and social behavior in bats. Can we predict the patterns of social cooperation across different species based on ecological factors and life history traits? Is kinship less important for shaping cooperation among bats compared to other social taxa, and if so, why? What mechanisms prevent cheating in helping behaviors such as food sharing and pup guarding? To what extent do bats form long-term social bonds or follow particular conspecifics when foraging, dispersing, or migrating? Have social bat species converged on behaviors found in other highly cognitive social mammals? How does social behavior correlate with brain morphology? Do social networks among bats predict social transmission of pathogens and parasites?

The social lives of bats often play out in dark, elusive places, and the extent of direct observations of bat social behavior therefore pales in comparison to those of group-living primates, birds, and diurnal mammals. For bats, occasional observations of roosting aggregations may not be sufficient to reveal the full extent of social relationships. For example, fission–fusion dynamics lead to highly associated bats being in different roosts (e.g., Wilkinson 1985; Patriquin et al. 2010; Kerth et al. 2011), and large cave colonies might conceal smaller cryptic social networks or groups of highly associated individuals. Further advances in the tracking of individuals through PIT and GPS tags will surely lead to great advances in quantifying social network structure in bats. However, direct observation of the social behavior of marked individuals, albeit difficult, can lead to significant insight into cooperation and conflict in bats.

Acknowledgments GGC thanks the support of a Ford Foundation Predoctoral Fellowship. GSW thanks the National Science Foundation for supporting studies on bat social behavior conducted by himself and his past students, JW Boughman and KM Bohn.

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