

Does food sharing in vampire bats demonstrate reciprocity?

Gerald Carter* and Gerald Wilkinson

University of Maryland; College Park, MD USA

Keywords: cooperation, food sharing, reciprocity, vampire bats

Claims of reciprocity (or reciprocal altruism) in animal societies often ignite controversy because authors disagree over definitions, naturalistic studies tend to demonstrate correlation not causation, and controlled experiments often involve artificial conditions. Food sharing among common vampire bats has been a classic textbook example of reciprocity, but this conclusion has been contested by alternative explanations. Here, we review factors that predict food sharing in vampire bats based on previously published and unpublished data, validate previous published results with more precise relatedness estimates, and describe current evidence for and against alternative explanations for its evolutionary stability. Although correlational evidence indicates a role for both direct and indirect fitness benefits, unequivocally demonstrating reciprocity in vampire bats still requires testing if and how bats respond to non-reciprocation.

Introduction

In human societies, cooperative behaviors such as food sharing^{1,2} are often enforced by reciprocity. By making small sacrifices to help certain individuals in need, humans consciously or unconsciously make strategic social investments that strengthen social relationships in the short term and yield reciprocal benefits in the long-term. Such reciprocity requires that cooperative investments are contingent on cooperative returns. As a result, cooperative behavior leads to higher fitness gains than more selfish behavior.

Claims of reciprocity in nonhuman animals, however, are controversial for several reasons. Authors disagree on what key properties define reciprocity.³⁻⁵ Naturalistic field studies tend to demonstrate correlations but not contingency between helping acts, and most controlled experiments involve helping acts with trivial costs or that require training, making their interpretation difficult.^{4,5}

Perhaps most importantly, reciprocity in social vertebrates may be embedded within complex social relationships. Decades of studies on primate cooperation suggest that cooperative behaviors

like food sharing and social grooming are based on social bonds that are reciprocal over the long-term but do not necessarily involve strictly contingent short-term tit-for-tat exchanges.^{3,6-8} Experimental demonstrations of contingent reciprocity are difficult under these social conditions because the importance of single events may be overshadowed by a foundation of past cooperative behaviors, which are often difficult to manipulate under natural conditions.^{1,3,8} A further complication is that individuals may exchange different kinds of services, and exchange rates may differ based on social status or access to resources.⁹

One of the early classic examples of non-human reciprocity is the regurgitation of blood among female common vampire bats (*Desmodus rotundus*).¹⁰ Food sharing among vampire bats might represent a powerful non-primate model for testing mechanisms of reciprocity because it is energetically costly to donors yet voluntary, and it is natural yet relatively easy to induce and measure. Moreover, reciprocal food sharing occurs between both kin and non-kin vampire bats, and may provide both direct and indirect fitness benefits.^{10,11} The reciprocity hypothesis for vampire bat food sharing has, however, become increasingly contested.^{4,12-17} In a recent study,¹¹ we addressed some, but not all, of the alternative explanations for food sharing. Here, we review the known correlates of food sharing in vampire bats using both previously published and unpublished data, briefly discuss various definitions of the term reciprocity, and then describe evidence for and against various explanations for why vampire bats share food.

Correlates of Food Sharing in Vampire Bats

Kinship. Regurgitated food sharing in common vampire bats (*Desmodus rotundus*) was first noticed between mothers and pups in captivity,¹⁸ but was later recognized as an important social behavior among adults in a field study conducted in Costa Rica from 1978 to 1983.¹⁰ Here, vampire bats frequently switched between several roost trees and co-roosted with kin and non-kin. Mean kinship (relatedness) estimates within roosting groups were estimated at $r = 0.03-0.11$,¹⁹ yet 95% of food sharing observed in the wild occurred between close kin ($r > 0.2$). Out of 110 food-sharing observations, 70% were mothers feeding their pups ($r = 0.5$). Of the 21 remaining non-maternal sharing events where kinship and co-roosting associations were known, 16 involved close kin ($r = 0.25$ or greater) and only one involved non-kin.¹⁰

*Correspondence to: Gerald Carter; Email: gcarter@umd.edu

Submitted: 06/04/13; Revised: 07/16/13; Accepted: 07/16/13

Citation: Carter G, Wilkinson G. Does food sharing in vampire bats demonstrate reciprocity? *Commun Integre Biol* 2013; 6: e25783; <http://dx.doi.org/10.4161/cib.25783>

Table 1. Captive fasting trials with 8 groups of common vampire bats

Bats	Previous association	Kinship estimate (mean+/-SD, range)	Begging or sharing?*	Source
5 females	Unfamiliar bats caught at different locations in Trinidad then placed together for 6 d	0.05 +/- 0.08**, 0-0.19 (25 loci)	No begging after 6 d, begging only at 21 and 36 d	Unpublished
6 females	Captured together in mist nets from one location in Trinidad	0.02 +/- 0.04, 0-0.14 (25 loci)	Begging only	Unpublished
5 females	Captured together in a mist net from one site in Belize	0.03 +/- 0.07, 0-0.23 (22 loci)	Begging only	Unpublished
6 females, 1 male	Captured together from same roost tree in Trinidad	0.04 +/- 0.06, 0-0.26 (25 loci)	Begging only	Unpublished
8 females, 1 male	Known frequent roostmates from a site in Costa Rica	0.01 +/- 0.06, 0-0.25 (maternal pedigree)	Yes	Wilkinson, 1984
4 females, 2 males	Long-term captivity	0.15 +/- 0.06, (maternal pedigree)	Yes	DeNault and McFarlane, 1995
9 females, 16 males	Long-term captivity	0.06 +/- 0.10, 0-0.58 (25 loci)	Yes	Carter and Wilkinson, 2013
6 females, 1 male	Long-term captivity	0.14 +/- 0.14, 0-0.46 (25 loci)	Yes	Unpublished

*Begging is defined as the fasted subject licking the mouth of a conspecific; sharing involves the same plus subsequent weight gain in the fasted subject. **Note that bats sampled randomly from a wild population should have zero relatedness.

These observations suggest that vampire bats are capable of kin discrimination and that food sharing elevates indirect fitness.

Association. Even after controlling for kinship, non-maternal food sharing was also explained by frequency of interaction; in all 21 non-maternal cases, co-roosting association was greater than 60%.¹⁰ Association also predicted non-kin regurgitations in a captive fasting experiment where 9 bats from two different populations were housed together.¹⁰ In these experiments, bats selected from the same population were frequent roost-mates, and only one pair was related. A random bat was deprived of food each night, then placed with others that had been fed and observed for 2 h, and this was repeated until all bats had been fasted at least twice. Fasted bats were weighed before and after the 2 h period to determine mass gain. Fasted bats were fed by bats from the same population in 12 of the 13 observed cases of food sharing, while sharing across populations occurred once.

From 2010 to 2013, we have repeated this fasting experiment with several groups of common vampire bats that were either captive-born or captured from the wild at the same or different locations (Table 1). Overall, fasting trials induced food sharing more often among frequent roostmates and long-term captive bats than those caught from the same roost or area with unknown associations (Table 1), which is consistent with the hypothesis that food sharing requires long-term associations.

In particular, previously unpublished data from 2010 suggests that food sharing may require social bonds that require development over long periods of time. In Trinidad, we captured 5 females at 5 sites that were 20–90 km apart. We conducted 3 separate food-sharing experiments to see if these previously unfamiliar individuals would begin sharing food after being kept in captivity together for several weeks. To assess changes in allogrooming over time, we also conducted random focal sampling of allogrooming. We ranked the amount of time each bat spent grooming others, then tested whether the mean ranks across bats increased over time using a permutation test (*lmPerm* package in R). We never observed food sharing, but we found that bats began begging others on the second and third sets of fasting trials on days 21 and 36 (Table 1). We also found that allogrooming increased over time among the previously unfamiliar bats [$R^2 = 0.45$, $F(1,10) = 8.3$, $p = 0.018$].

We conducted other trials with groups of female common vampire bats that may have been previously familiar. Two groups in Trinidad and Belize were captured flying in close proximity (in the same mist net within a roughly 5 min period). We tested another group of vampire bats captured from the same tree hollow in Trinidad, but again with unknown levels of association. In all 4 groups ($n = 48$ fasting trials), we observed some begging but no food sharing.

Table 2. Factors predicting food sharing in vampire bats

Study	No. donations	No. bats	Co-roosting association	Kinship	Reciprocal help
Wilkinson (1984) field data	110	184	Yes	Yes	?
Wilkinson (1984) captive data	13	9	Yes	Controlled at 0	Yes
DeNault and McFarlane (1995)	10	6	Controlled at 100%	No	?
Carter and Wilkinson (2013)	204	25	Controlled at 100%	Not after controlling other factors	Yes

In sharp contrast, we observed food sharing consistently among kin and non-kin that have been housed together in long-term captivity (Table 1). Under these conditions, all females are generally fed when fasted, including females born in different populations but housed with others for multiple years (discussed below). Although observations of food sharing have been mostly restricted to groups with known levels of high association, sharing between bats from different populations has also been observed once in Costa Rica.¹⁰ Therefore, factors other than previous association, such as variations in behavior due to geographic origin or stress, might also explain the presence or absence of food sharing across these groups (Table 1).

A final line of evidence that association influences food sharing is that male vampire bats do not form stable associations nor share food in the wild, but they do share food in captivity where associations are stable.²⁰ In a 1995 study with 10 captive vampire bats, DeNault and McFarlane²⁰ found that 2 adult males that were related ($r = 0.26$) roosted in close proximity, performed mutual allogrooming, and both donated and reciprocated food. The authors failed however to find a correlation between kinship and presence of food sharing across all bats.

Reciprocal help. The amount of food given from bat A to bat B is predicted by the amount of food given from bat B to A. This latter value can be measured in at least 2 ways. For predicting the food sharing rate from bat A to B, a predictor we call “reciprocal help” is the average sharing rate from B to A over the longest possible time span. In contrast, for predicting food given from A to B at a given trial, a predictor we call “past help” is the presence or amount of food given from B to A in one or more previous trials. Past help should predict food sharing if the helping decisions of bats are determined by recent past social experience, whereas reciprocal help should predict food sharing even better if bats accrue social information over longer time periods.

In the 1984 study,¹⁰ 6 opportunities were created where a captive fasted bat could have been fed by unrelated bats that it fed previously, and this occurred 4 times, more than expected by chance. In this captive experiment, past help predicted donations but only when kin were absent, while in previous field observations, kinship predicted donations but all cases of reciprocal help were not known (Table 2). Therefore, the roles of reciprocal help and kinship could not be tested simultaneously in the original study.¹⁰

In a more recent 2013 study,¹¹ we tested the relative roles of reciprocal help and kinship, by inducing 204 cases of food-sharing in 20 common vampire bats of mixed sex (9 females) and kinship over a 2-y period. For all potential pairs that could share food, we estimated donation amounts by time spent mouth-licking (which strongly correlated with mass gained during the 2 h

trial, $r = 0.9$), and defined food sharing as the log-transformed donation rate from A to B, reciprocal help as the log-transformed donation rate from B to A, and kinship as the genetic relatedness estimate between A and B.¹¹ Some individuals originated from different captive populations, but all bats were housed in the same flight cage for several years. Under these conditions, we found that reciprocal help, but not kinship, predicted food sharing. Other predictors of food sharing included social grooming, donor sex, and a positive interaction between reciprocal help and kinship, which revealed that related pairs shared with even greater symmetry compared with less-related pairs.¹¹

In the original paper, we used 13 microsatellite loci to estimate kinship,¹¹ but we have since reanalyzed the data using more precise kinship estimates based on information from 25 variable microsatellite loci, and our conclusions have remained the same. Our new updated model (adjusted $R^2 = 0.38$, $F(5,306) = 37.0$) still includes reciprocal help ($\beta = 0.32$, $p < 0.0002$), donor sex ($\beta = 0.26$, $p < 0.0002$), allogrooming received ($\beta = 0.20$, $p < 0.0002$), and the interaction between kinship and reciprocal help ($\beta = 0.06$, $p = 0.04$) in the same order of relative importance. The model still does not include kinship ($\beta = 0.07$, $p = 0.6$).

Reciprocal help (averaged over all trials) predicted food sharing better than past help (in recent previous trials). In other words, reciprocity was most evident in the form of symmetrical helping across pairs rather than within pairs. We conducted a test of temporal contingency and found that the amount given from A to B in each trial correlated with the total amount previously given from B to A during the most recent donation. Yet, the correlation was weak ($r = 0.28$) and apparent only after controlling for the total amount received by the recipient in the trial.¹¹ Hungry bats were fed by an average of 4 partners per trial, and these were typically the same partners across repeated trials but not always. In summary, the bats did not perform strictly balanced exchanges in isolated pairs, and symmetry in sharing was most obvious over longer time spans as found in primate cooperation.^{3,8}

Do Vampire Bats Exhibit Reciprocity?

Definitions. Answering this question requires crossing an unfortunate semantic quagmire. Definitions of reciprocity have varied greatly over time and between authors^{3-6,21-24} ever since Trivers²¹ first described “reciprocal altruism” (now widely recognized as a misnomer since reciprocal altruism enforces mutual benefit). In this paper, Trivers²¹ implicitly lumped all helping behaviors yielding future direct fitness benefits into his definition, but he later clarified reciprocal altruism as a special case of this broader category.²⁵

The broadest definitions of reciprocity are based on observed outcomes. For example, some authors use reciprocity to refer merely to correlations between help given and received when controlling for kinship,²⁶ or in other cases even when such helping is based on kinship (e.g., “symmetry-based reciprocity”).^{27,28} Food sharing in vampire bats clearly fits these very broad definitions. On the other end of the spectrum are very narrow definitions. For instance, some authors suggest reciprocity requires planned investments and expected returns where “individuals must choose between the immediate reward of defecting and the long-term reward of cooperating.”¹²

Some authors distinguish between positive reciprocity (rewarding cooperators) and negative reciprocity (punishing cheats), or between reciprocity (where costly cooperative investments are made by both partners) and pseudoreciprocity (where costly investment by one partner leads to a non-costly byproduct benefit from the other).^{4,29} Such distinctions can be useful in some contexts, but can also create confusion. For example, many reciprocity definitions require showing that a helping act poses not only energetic costs but also “net fitness costs at the time it is provided in natural populations.”⁴ Helping behaviors typically pose some energetic cost, but there is no putative case of cooperation where this “temporary fitness cost” has been demonstrated.⁴ Indeed, it is unclear how an experimenter could clearly demonstrate that an adaptive helping behavior (which increases expected lifetime fitness by definition) somehow simultaneously decreases expected lifetime fitness temporarily during the social interaction.

For our purposes, we define reciprocity broadly as “a conditional enforcement strategy where individuals preferentially help partners that reciprocate and withhold help to partners that do not.” Importantly, such enforcement could occur through partner choice, partner control strategies or both, since either mechanism leads to an outcome that rewards cooperation and punishes cheating.^{5,6,9,30-34} This operational definition implies an ultimate-level function because the necessity to contingently adjust cooperative investments is an expected design feature if investments pose fitness costs and cheating has created selective pressure to enforce cooperation. Finally, this definition clarifies exactly what is still needed to demonstrate reciprocity: an experimental test of whether bats will decrease aid to partners that are rendered unable to reciprocate.

Partner choice or partner control. Reciprocity defined in this broad way is synonymous with the enforcement of mutual benefits,²⁴ a phenomenon that has been well-demonstrated in interspecific mutualisms. For example, both plants and their mycorrhizal fungal symbionts prefer to exchange nutrients with partners that offer the best returns on investment.³⁵ In some cases, reciprocity might occur primarily through partner choice. Biological markets^{30,31} often result when different types of organisms have access to different resources, and at least one type can choose among several exchange partners. In this case, reciprocity may occur primarily through partner choice and partner switching. The more partners are locked into a repeated dyadic interaction, the more likely that enforcement will take the form of partner control (reward and punishment of the same partner over time). Testing

the relative importance of partner control and partner choice in vampire bats would be difficult, and would involve comparing how bats respond to non-reciprocation in both the presence and absence of alternative partners.

Resource exchange markets should be less common between conspecifics, which have access to the same pool of resources, but such models can still apply to vampire bats for two reasons. First, one cooperative service, such as grooming, can be traded for others, as found in primates.^{7-9,36} This possibility could be verified by testing if a partner that is unable to reciprocate food donations compensates by increasing time spent grooming. Second, even if blood is only exchanged for blood, its value for each vampire bat fluctuates largely over a 24 h period and differs drastically depending on whether that individual has fed successfully.¹⁰ This is because, like social carnivores that hunt cooperatively, vampire bats typically acquire either a large meal or none at all. Unlike social hunters however, vampire bats usually feed individually rather than as a group, and blood may be easier to share at the roost than at the wound site. It is worth noting however that vampire bats have also been observed both fighting and feeding at the same wound.¹⁹

The Social Bond Hypothesis

If we assume that non-kin food sharing is adaptive, then its evolutionary stability requires that bats cannot exploit food sharing by receiving donations while donating less than average amounts to others in need (i.e., cheating). One hypothesis is that cheating is prevented by both kin discrimination and enforcement through reciprocity.^{10,23} This hypothesis predicts that bats should discriminate between kin and non-kin, but also between 2 equally related partners that yield different cooperative returns.

Such dual enforcement could occur through long-term, kin-biased social bonds. If bats form social bonds that provide mostly direct, but also indirect fitness benefits, and if the adaptive value of social bonds is actively enforced by reciprocity, then several observations can be explained.²³ First, this would explain why kinship predicts sharing in wild bats (where such bonds may typically form among kin), but not in captive bats when controlling for association, social grooming, and reciprocal help.¹¹ Second, it would explain why the food-sharing network in both captive and wild vampire bats is female-biased, symmetrical, consistent, and correlated with mutual social grooming. Finally, complex social bonds as found in some primates,⁷ could also help explain why vampire bats are outliers for residual brain and neocortex size among bats.^{37,38}

The social bond hypothesis for food sharing predicts that vampire bats will make cooperative investments of different types (e.g., social grooming, tolerance for feeding at the same source) within the same food-sharing partners over time, alter these cooperative investments slowly depending on how the cooperative returns compare with other individuals (partner choice) and past returns (partner control), and compensate for inability to reciprocate food sharing by increasing other services, such as social grooming. Finally, food sharing manipulation should be possible not only by controlling social experiences, but also

by direct manipulation of hormonal and neural mechanisms of social bonding.

Alternative Explanations

Several alternative models of vampire bat food sharing assume that enforcement of cooperation is not necessary. One example is pseudoreciprocity,^{13,39} which assumes that food sharing is stable because it ensures the survival of roost-mates that are valuable for providing some byproduct service such as broadcasting social information about prey locations^{40,41} or for keeping offspring warm.⁴² But even in these scenarios subtle cheating may be possible.⁴³

Another suggestion is that non-kin food sharing is manipulation not cooperation.⁴ Harassment often plays an important role in primate sharing,^{7,44,45} but is unlikely to strongly influence food sharing in vampire bats because begging bats are easily rejected and donors initiate the majority of food-sharing bouts by approaching, grooming, and licking the mouth of hungry subjects.¹¹

Multilevel selection models of vampire bat food sharing argue that neither kin discrimination nor reciprocity is needed to stabilize food sharing, because cooperative genotypes can assort themselves passively without enforcement behaviors.^{14,16,17} To explain these scenarios from an inclusive fitness perspective, indiscriminate sharing within roosts is expected to provide indirect fitness benefits as long as the average within-roost kinship exceeds 0.05.¹⁴ If helping nearby non-kin is simply less costly to inclusive fitness than allowing kin to starve, then selection can favor indiscriminate or imprecise kin altruism based on proximity, association, or familiarity. This is especially likely when limited dispersal is typical under natural conditions.⁴⁶ It is then possible that these symmetrical, but imprecise, cues also lead to symmetrical helping in captivity.

These models face several problems. Kin-biased sharing in adult wild bats is still evident after controlling for association.¹⁰ Food sharing relationships are consistent and non-random within groups.¹¹ Furthermore, both theory and comparative evidence⁴⁶ predict the evolution of strong kin discrimination under the socioecological conditions faced by vampire bats. Specifically,

food sharing poses a large benefit to recipients, and kinship between donors and possible recipients has a low mean and high variance.^{10,19} Hence, indiscriminate sharing within roosts is unlikely to be evolutionarily stable when individuals vary in cooperativeness or against enforcement strategies such as kin discrimination or reciprocity.

If we instead assume vampire bats can discriminate among kin, but do not exhibit reciprocity, then it is difficult to explain why reciprocal help, but not kinship, predicts food sharing under captive conditions unless long-term captivity somehow disrupts natural kin discrimination behavior. In summary, alternative explanations can make fewer assumptions, but not without explaining less of what we know about vampire bat food sharing.

Conclusion

Evidence for kin discrimination often relies on correlational evidence without demonstration of exact mechanisms, yet skeptics of reciprocity increasingly require far more stringent evidence than mere correlation or even contingency.^{3,4,6,12} Vampire bats demonstrate symmetrical exchanges of help, but it has yet to be demonstrated that vampire bats use conditional enforcement to prevent cheating. There are two obvious gaps in knowledge. First, can vampire bats discriminate kin when past association is controlled? Second, do bats change investments based on cooperative returns? Additional experiments answering these questions should provide valuable insight into the mechanisms that maintain food sharing in these intriguing animals.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Acknowledgments

We thank Frantisek Baluska for inviting us to write this paper. Ronald Noe and an anonymous reviewer provided helpful comments. Lauren Leffer, Micah Miles, and Adi Shaked helped with data collection. New work described here was supported by grants from the Cosmos Club Foundation, Sigma Xi, the American Society of Mammalogy, and with permission of the Trinidad Forestry Division, Wildlife Section.

References

1. Gurven M. To give and to give not: the behavioral ecology of human food transfers. *Behav Brain Sci* 2004; 27:543-59; <http://dx.doi.org/10.1017/S0140525X04000123>
2. Gurven M. The evolution of contingent cooperation. *Curr Anthropol* 2006; 185-192.
3. Schino G, Aureli F. Reciprocal altruism in primates: partner choice, cognition, and emotions. *Adv Stud Behav* 2009; 39:45-69; [http://dx.doi.org/10.1016/S0065-3454\(09\)39002-6](http://dx.doi.org/10.1016/S0065-3454(09)39002-6)
4. Clutton-Brock T. Cooperation between non-kin in animal societies. *Nature* 2009; 462:51-7; PMID:19890322; <http://dx.doi.org/10.1038/nature08366>
5. Noë R. Cooperation experiments: coordination through communication versus acting apart together. *Anim Behav* 2006; 71:1-18; <http://dx.doi.org/10.1016/j.anbehav.2005.03.037>
6. Schino G, Aureli F. A few misunderstandings about reciprocal altruism. *Commun Integr Biol* 2010; 3:561-3; PMID:21331239; <http://dx.doi.org/10.4161/cib.3.6.12977>
7. Silk JB, Brosnan SF, Henrich J, Lambeth SP, Shapiro S. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Anim Behav* 2013; 85:941-7; <http://dx.doi.org/10.1016/j.anbehav.2013.02.014>
8. Jaeggi AV, De Groot E, Stevens JMG, Van Schaik CP. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evol Hum Behav* 2013; 34:69-77; <http://dx.doi.org/10.1016/j.evolhumbehav.2012.09.005>
9. Fruteau C, Voelkl B, van Damme E, Noë R. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc Natl Acad Sci USA* 2009; 106:12007-12; PMID:19581578; <http://dx.doi.org/10.1073/pnas.0812280106>
10. Wilkinson GS. Reciprocal food sharing in the vampire bat. *Nature* 1984; 308:181-4; <http://dx.doi.org/10.1038/308181a0>
11. Carter GG, Wilkinson GS. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc R Soc B Biol Sci* 2013; 280 (doi: 10.1098/rspb.2012.2573).
12. Stevens JR, Cushman FA, Hauser MD. Evolving the psychological mechanisms for cooperation. *Annu Rev Ecol Syst* 2005; 36:499-518; <http://dx.doi.org/10.1146/annurev.ecolsys.36.113004.083814>
13. Connor RC. Cooperation beyond the dyad: on simple models and a complex society. *Philos Trans R Soc Lond B Biol Sci* 2010; 365:2687-97; PMID:20679112; <http://dx.doi.org/10.1098/rstb.2010.0150>
14. Foster KR. Diminishing returns in social evolution: the not-so-tragic commons. *J Evol Biol* 2004; 17:1058-72; PMID:15312078; <http://dx.doi.org/10.1111/j.1420-9101.2004.00747.x>
15. Davies NB, Davies NB, Krebs JR, West SA. An introduction to behavioural ecology. West Sussex, UK: Wiley-Blackwell; 2012.

16. Paolucci M, Conte R, Tosto GD. A model of social organization and the evolution of food sharing in vampire bats. *Adapt Behav* 2006; 14:223-38; <http://dx.doi.org/10.1177/105971230601400305>
17. Witkowski M. Energy sharing for swarms modeled on the common vampire bat. *Adapt Behav* 2007; 15:307-28; <http://dx.doi.org/10.1177/1059712307082092>
18. Schmidt U, Manske Uwe. Die Jugendentwicklung der Vampirfledermause (*Desmodus rotundus*). *Z Saugetierkd* 1973; 38:14
19. Wilkinson G. The social organization of the common vampire bat I and II. *Behav Ecol Sociobiol* 1985; 17:111-34
20. DeNault LK, McFarlane DA. Reciprocal altruism between male vampire bats, *Desmodus rotundus*. *Anim Behav* 1995; 49:855-6
21. Trivers R. The evolution of reciprocal altruism. *Q Rev Biol* 1971; 46:35-57; <http://dx.doi.org/10.1086/406755>
22. Koenig W. Reciprocal altruism in birds: a critical review. *Ethol Sociobiol* 1988; 9:73-84; [http://dx.doi.org/10.1016/0162-3095\(88\)90014-3](http://dx.doi.org/10.1016/0162-3095(88)90014-3)
23. Wilkinson G. Reciprocal altruism in bats and other mammals. *Ethol Sociobiol* 1988; 9:85-100; [http://dx.doi.org/10.1016/0162-3095\(88\)90015-5](http://dx.doi.org/10.1016/0162-3095(88)90015-5)
24. West SA, Griffin AS, Gardner A. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J Evol Biol* 2007; 20:415-32; PMID:17305808; <http://dx.doi.org/10.1111/j.1420-9101.2006.01258.x>
25. Trivers R. Reciprocal altruism: 30 years later. In: Kappeler PDP, Schaik PDCP van, eds. *Cooperation in Primates and Humans*. Berlin: Springer Heidelberg; 2006: 67-83.
26. Schino G, Aureli F. The relative roles of kinship and reciprocity in explaining primate altruism. *Ecol Lett* 2010; 13:45-50; PMID:19840082; <http://dx.doi.org/10.1111/j.1461-0248.2009.01396.x>
27. Brosnan SF, De Waal F. A proximate perspective on reciprocal altruism. *Hum Nat* 2002; 13:129-52
28. De Waal F, Brosnan S. Simple and complex reciprocity in primates. In: Kappeler PM, van Schaik CP, ed. *Cooperation in Primates and Humans: Mechanisms and Evolution*. New York: Springer, 2006:85-105.
29. Bergmüller R, Johnstone RA, Russell AF, Bshary R. Integrating cooperative breeding into theoretical concepts of cooperation. *Behav Processes* 2007; 76:61-72; PMID:17703898; <http://dx.doi.org/10.1016/j.beproc.2007.07.001>
30. Noë R, Hammerstein P. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol* 1994; 35:1-11; <http://dx.doi.org/10.1007/BF00167053>
31. Noë R, Hammerstein P. Biological markets. *Trends Ecol Evol* 1995; 10:336-9; PMID:21237061; [http://dx.doi.org/10.1016/S0169-5347\(00\)89123-5](http://dx.doi.org/10.1016/S0169-5347(00)89123-5)
32. Fruteau C, Lemoine S, Hellard E, van Damme E, Noë R. When females trade grooming for grooming: testing partner control and partner choice models of cooperation in two primate species. *Anim Behav* 2011; 81:1223-30; <http://dx.doi.org/10.1016/j.anbehav.2011.03.008>
33. Bshary R, Bronstein JL. A general scheme to predict partner control mechanisms in pairwise cooperative interactions between unrelated individuals. *Ethology* 2011; 117:271-83; <http://dx.doi.org/10.1111/j.1439-0310.2011.01882.x>
34. Krams I, Krama T, Igaune K, Mänd R. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behav Ecol Sociobiol* 2008; 62:599-605; <http://dx.doi.org/10.1007/s00265-007-0484-1>
35. Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, et al. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 2011; 333:880-2; PMID:21836016; <http://dx.doi.org/10.1126/science.1208473>
36. Barrett L, Henzi SP. The utility of grooming in baboon troops. In: Noë, R, van Hooft, JARAM, Hammerstein P, eds. *Economics in Nature. Social Dilemmas, Mate Choice and Biological Markets*. Cambridge: Cambridge University Press, 2001: 119-145.
37. Baron G, Stephan H, Frahm HD. *Comparative neurobiology in Chiroptera*. 1996; Berlin: Birkhauser.
38. Dunbar RIM, Shultz S. Evolution in the social brain. *Science* 2007; 317:1344-7; PMID:17823343; <http://dx.doi.org/10.1126/science.1145463>
39. Connor RC. Pseudo-reciprocity: Investing in mutualism. *Anim Behav* 1986; 34:1562-6; [http://dx.doi.org/10.1016/S0003-3472\(86\)80225-1](http://dx.doi.org/10.1016/S0003-3472(86)80225-1)
40. Wilkinson GS. Information transfer at evening bat colonies. *Anim Behav* 1992; 44:501-18; [http://dx.doi.org/10.1016/0003-3472\(92\)90059-1](http://dx.doi.org/10.1016/0003-3472(92)90059-1)
41. Safi K, Kerth G. Comparative analyses suggest that information transfer promoted sociality in male bats in the temperate zone. *Am Nat* 2007; 170:465-72; PMID:17879196; <http://dx.doi.org/10.1086/520116>
42. Kokko H, Johnstone RA, Clutton-Brock TH. The evolution of cooperative breeding through group augmentation. *Proc Biol Sci* 2001; 268:187-96; PMID:11209890; <http://dx.doi.org/10.1098/rspb.2000.1349>
43. Haig D. Huddling: brown fat, genomic imprinting and the warm inner glow. *Curr Biol* 2008; 18:R172-4; PMID:18302923; <http://dx.doi.org/10.1016/j.cub.2007.12.040>
44. Stevens JR. The selfish nature of generosity: harassment and food sharing in primates. *Proc Biol Sci* 2004; 271:451-6; PMID:15129953; <http://dx.doi.org/10.1098/rspb.2003.2625>
45. Gilby IC. Mear sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim Behav* 2006; 71:953-63; <http://dx.doi.org/10.1016/j.anbehav.2005.09.009>
46. Cornwallis CK, West SA, Griffin AS. Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. *J Evol Biol* 2009; 22:2445-57; PMID:19824927; <http://dx.doi.org/10.1111/j.1420-9101.2009.01853.x>