ABSTRACT

Title of dissertation: **COOPERATION AND SOCIAL BONDS IN COMMON VAMPIRE BATS**

Gerald G. Carter, Ph.D., 2015

Dissertation directed by: Professor Gerald S. Wilkinson
Department of Biology

Regurgitated food sharing among vampire bats is a classic textbook example of reciprocity ("reciprocal altruism"). But many authors have contested both the notion that reciprocity explains vampire bat food-sharing and the importance of reciprocity more generally. In Chapter 1, I review the literature on evolutionary explanations of cooperation. I show why reciprocity was once considered important but is now considered rare: overly literal translations of game theory strategies have resulted in problems for both defining and testing reciprocity. In Chapter 2, I examine the relative roles of social predictors of food-sharing decisions by common vampire bats (*Desmodus rotundus*) under controlled conditions of mixed relatedness and equal familiarity by fasting 20 individuals in 48 trials over two years. The food-sharing network was consistent, symmetrical, and correlated with mutual allogrooming. Non-kin food-sharing patterns were not consistent with harassment or byproduct explanations. I next attempted to manipulate food-sharing decisions in two ways. In Chapter 3, I administered intranasal oxytocin to test for effects on allogrooming and food sharing. I observed that inhaled oxytocin slightly increased the magnitude of food donations within dyads, and the amount of female allogrooming within and across all partners, without increasing number of partners. In Chapter 4, I assessed contingency of food-sharing in 7 female dyads (including four pairs of mother and adult daughters) with prior histories of sharing. To test for evidence of partner switching, I measured dyadic levels of food sharing before and after a treatment period where I prevented dyadic sharing (each bat could only be fed by others). A bat’s sharing network size predicted how much food it received in the experiment. When primary donors were excluded, subjects did not compensate with donations from other partners. Yet, food-sharing bonds appeared unaffected by the non-sharing treatment. In particular, close maternal kin were clearly not enforcing cooperation using strict contingency. I argue that any contingencies within such bonds are likely to involve multiple services and long timescales, making them difficult to detect. Simple and dyadic ‘tit-for-tat’ models are unlikely to predict cooperative decisions by vampire bats or other species with stable, mixed kinship, social bonds.

COOPERATION AND SOCIAL BONDS IN COMMON VAMPIRE BATS

by

Gerald Gunnawa Carter

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2015

Advisory Committee:
Professor Gerald Wilkinson, Chair
Professor Gerald Borgia
Associate Professor Karen Carleton
Associate Professor Matthew Roesch
Adjunct Professor Katerina Thompson

Preface

Chapter 1 was previously published in 2014 as “The reciprocity controversy” in *Animal Behavior and Cognition* (vol 1, 368-386). Chapter 2 was published in 2013 as “Food sharing in vampire bats: Reciprocal help predicts donations more than relatedness or harassment” in *Proceedings of the Royal Society B: Biological Sciences* (vol 280, 20122573). Chapters 3 and 4 are in manuscript form. The Introduction and Appendix 1 includes altered text and tables from the article “Does food sharing in vampire bats demonstrate reciprocity?” published in *Communicative & Integrative Biology* (vol *6*., e25783). Appendix 2 is published as an online supplement to the paper published as Chapter 2. Appendix 3 and 4 are written as potential online supplements for the manuscripts corresponding to Chapters 3 and 4.

Dedication

To all my friends at The Organization for Bat Conservation who generously supported my work.

Acknowledgements

My work was generously supported by the Organization for Bat Conservation, and would not have been possible without logistical and moral support from the people there including Rob Mies, Jessica Fabian, Amanda Felk, Christina Funk, Dawn Vezina, and Erica Antishin. I thank Lauren Leffer, Erik Kim, Micah Miles, and Adi Shaked for assisting me with data collection. Rob Fleischer and Nancy Rotzel provided me with next-generation 454 DNA sequences. I also thank Jennifer Vonk, Jason Watters, Jeffrey Mitchell, Julie Samy, Danielle Adams, Edward Hurme, Kyle Miller-Hesed, and Josie Reinhardt, and my advisory committee. Most of all, I have been supported by my loving wife Michelle Nowak.

For this project, I stood on the shoulders of many giants. I’ve learned more from Jerry Wilkinson than any advisor. It’s been humbling to read his doctoral work and see what he achieved over three decades ago, before so many of today’s theoretical and technological advances, using pure ingenuity and hard work.

The Ford Foundation awarded me a three-year Predoctoral Fellowship. My work was funded by grants from the Cosmos Club Foundation, American Society of Mammalogists, Explorer's Club Washington Group, Sigma Xi, Animal Behavior Society; a Dissertation Improvement Grant from the National Science Foundation; and donations from Mary Smith, Matthew Mulkeen, and 57 other donors on petridish.org.

Table of Contents

List of Tables

List of Figures

Introduction

What are the evolutionary advantages of helping others? This question has been central to evolutionary biology since Darwin (1871) first realized that altruistic, non-reproductive workers in eusocial insect societies posed a "special difficulty" to his theory of natural selection (see an excellent review by Ratnieks et al. 2011). The puzzle of altruism was solved by Hamilton's (1964) inclusive fitness theory. But it took almost another decade for evolutionary biologists to realize that non-altruistic mutually beneficial cooperation led to its own, perhaps even more vexing, puzzle (Trivers 1971, Axelrod & Hamilton 1981). Inclusive fitness theory explains that helping between non-kin must yield direct fitness benefits, but not *how*. In many cases, cooperative traits or behaviors lead to a public good that can be exploited by less cooperative individuals, rendering the cooperative trait evolutionarily unstable unless there is mechanism for preventing such freeloading or "cheating" (West et al. 2007, Ghoul et al. 2013). This situation has been explained using the "prisoner's dilemma" and "snowdrift game" for two individuals or the "tragedy of the commons" for a group of individuals (e.g. Axelrod & Hamilton 1981, Dugatkin 1997, Foster 2004, Doebeli & Hauert 2005, West et al. 2007).

One solution to the prisoner's dilemma is repeated interactions combined with reciprocity or "reciprocal altruism" (Trivers 1971, Axelrod & Hamilton 1981). This is most obvious in human societies, where cooperative behaviors such as food sharing are often enforced by reciprocity (Trivers 1971, Gurven 2004, 2006). By making small sacrifices to help certain individuals, 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 ultimately contingent on cooperative returns.

One of the earliest and most classic empirical examples of reciprocity is food sharing by regurgitation of blood among common vampire bats (*Desmodus rotundus*). When adult female or young vampire bats miss a nightly meal, female roostmates will typically regurgitate some of their own blood meal to feed them (Wilkinson 1984). Field observations show that female donors regurgitate food mostly for their own offspring (70% of cases) but also for other familiar adult females. This adult sharing is predicted independently by both relatedness and co-roosting association (Wilkinson 1984). Reciprocal food sharing in vampire bats is frequently cited as an example of reciprocity, but it also demonstrates kin discrimination; despite the majority of possible donors being unrelated, more than 95% of food sharing occurred between close relatives ($r < 0.25$, Wilkinson 1984). On the other hand, a fasting experiment showed that reciprocal sharing also readily occurs among non-kin, suggesting that the bats might base their helping decisions on past social experience of help rather than only relatedness cues (Wilkinson 1984). Simulations show that, if help is indeed based on association, the resulting direct fitness benefits would greatly exceed the indirect fitness (kin-selected) benefits (Wilkinson 1988). But 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 an attempt by each bat to maintain its group’s size (Davies et al. 2012).

Claims of reciprocity in vampire bats, and in other nonhuman animals more generally, are controversial for several reasons. In Chapter 1, I review the literature on reciprocity and alternative evolutionary explanations of cooperation. I show that reciprocity was once considered important and widespread but is now considered rare for almost completely semantic reasons. Literal translations of the strategy ‘tit-for-tat’ in the repeated Prisoner’s Dilemma game have resulted in four problematic approaches to defining and testing reciprocity. I call these: *the calculated reciprocity error* (the assumption that reciprocity requires sophisticated cognitive abilities to plan ahead and properly discount future rewards), *the short-term contingency bias* (the idea that reciprocity must involve strict-turn-taking), *the temporary fitness cost paradox* (the requirement that tests of reciprocity show both the presence of cheating and that reciprocity prevents cheating), and finally, *the byproduct ambiguity* (the observation that any evidence for reciprocity can be reinterpreted post hoc as “pseudoreciprocity” where cooperative investments do not *cause* reciprocal cooperative returns, but merely *enable* them because no cheating exists).

In Chapter 2, I revisit the case of food sharing in vampire bats by examining social predictors of food-sharing decisions by common vampire bats (*Desmodus rotundus*) under controlled conditions of mixed relatedness and equal familiarity. I fasted 20 individuals in 48 trials over two years. I show that donors often greeted and initiated grooming and sharing with unfed bats; that the food-sharing network was consistent, symmetrical, and correlated with mutual allogrooming; that reciprocal help is a much stronger predictor of food sharing than kinship; and that non-kin sharing was common and not easily explained by proposed alternatives to the reciprocity hypothesis, such with harassment, group augmentation, or simple kin recognition errors. Results were consistent with the reciprocity hypothesis, but do not demonstrate contingency. Such a demonstration requires manipulating investments to elicit a behavioral response.

I attempted to manipulate food-sharing decisions in two ways. In Chapter 3, I administered intranasal oxytocin (OT) to test for increases in allogrooming and food sharing. There was no effect on the occurrence of sharing among dyads, but in the sharing events that did occur, I found that OT increased the magnitude of food donations within dyads, after controlling for dyad and amount of allogrooming. OT also increased the amount of female allogrooming per partner and across all partners, but not the number of partners. These results were promising, but suggested that OT treatments alone could not strongly manipulate food-sharing decisions.

In Chapter 4, I took a first step in the difficult tasking of testing contingency in reciprocal food sharing. Preliminary trials showed that vampire bat dyads and triads that always shared in the group setting of their home cage would not share food when isolated as dyads or triads in small cages, even after many days of habituation to the new setting. I therefore tested contingency using experimental dyads embedded in a group setting with multiple partners. I selected 7 female dyads (including four pairs of mother and adult daughters) with prior histories of sharing and tried to see if I could get these bats to invest more in other partners. To test for evidence of such partner switching, I measured dyadic levels of food sharing before and after a treatment period where dyadic sharing was prevented, because their paired donor was absent or unfed and each bat could only be fed by others. The size of a bat's sharing network predicted total food received in the experiment. When primary donors were excluded, subjects did not fully compensate with donations from other bats. After preventing dyadic sharing on 3 occasions over 3 weeks, food-sharing bonds appeared unaffected. In particular, close maternal kin were clearly not enforcing cooperation using strict contingency based on their most recent fasting experience.

Data from Chapter 4 are consistent with the idea from Chapter 1 that stable social bonds might influence reciprocity in several important ways. First, socially bonded individuals can integrate multiple cooperative services. For instance, evidence from primates suggests that imbalances in food sharing can be compensated by allogrooming (e.g. Fruteau et al. 2009). In vampire bats, food sharing is also predicted by allogrooming (Chapter 2, especially among non-kin: Chapter 4, Appendix 4), and sharing and allogrooming are influenced by a common hormonal mechanism (Chapter 3). Second, stable bonds should reduce the degree of contingency in the short-term and lengthen the timescale of reciprocation. In vampire bats, reciprocal patterns become stronger over longer timespans (Chapter 2), and sharing bonds are robust to recent periods of non-sharing (Chapter 4). Third, the value of social bonds and any constraint on the number of bonds an animal can maintain makes partner choice a potent force for stabilizing cooperation (Noë & Hammerstein 1994). Vampire bats with larger networks are more successful at obtaining food, primary partners are not quickly replaceable, and sharing bonds are stable to three successive non-sharing events (Chapter 4). Together, these results show that vampire bat cooperation involves many factors not included in the simple tit-for-tat model of reciprocity.

Chapter 1: The reciprocity controversy

Abstract

Reciprocity (or "reciprocal altruism") was once considered an important and widespread evolutionary explanation for cooperation, yet many reviews now conclude that it is rare or absent outside of humans. Here, I show that nonhuman reciprocity seems rare mainly because its meaning has changed over time. The original broad concept of reciprocity is well supported by evidence, but subsequent divergent uses of the term have relied on various translations of the strategy 'tit-for-tat' in the repeated Prisoner's Dilemma game. This model has resulted in four problematic approaches to defining and testing reciprocity. Authors that deny evidence of nonhuman reciprocity tend to (1) assume that it requires sophisticated cognition, (2) focus exclusively on short-term contingency with a single partner, (3) require paradoxical evidence for a temporary lifetime fitness cost, and (4) assume that responses to investments are fixed. While these restrictions basically define reciprocity out of existence, evidence shows that fungi, plants, fish, birds, rats, and primates enforce mutual benefit by contingently altering their cooperative investments based on the cooperative returns, just as predicted by the original reciprocity theory.

Introduction

Comparative psychologists, evolutionary psychologists, and behavioral ecologists often study cooperation using different theories and methods, asking questions at different levels of analysis. What cues trigger the cooperative behavior? How does it develop? When did it evolve? Why is it adaptive? The multidisciplinary nature of this field leads to new connections but also miscommunication. For instance, some semantic confusion occurs because comparative psychologists often define behaviors such as 'cooperation', 'altruism', and 'mutualism' based on proximate goals or motivations, similar to their colloquial usage (de Waal, 2008), whereas evolutionary biologists define these terms based on the ultimate net effects on direct fitness (i.e. lifetime reproductive success, West, Griffin, & Gardner, 2007a,b). Many misunderstandings resulting from these semantic discrepancies have been resolved elsewhere (see Noë, 2006, West, El Mouden, & Gardner, 2011; West et al., 2007b), but one important concept that continues to cause confusion is 'reciprocity' (or 'reciprocal altruism' Trivers, 1971).

Reciprocity is one of the best-known evolutionary explanations for cooperation, but also among the most controversial (Cheney, 2011; Clutton-Brock, 2009; Hammerstein, 2003; Schino & Aureli 2010a,b). Although once considered the key explanation for helping between non-kin, most reviews now conclude that it is absent or very rare outside of humans (e.g., Clutton-Brock, 2009; West et al., 2011). All claims of reciprocity have been disputed, including experimental evidence from fish (reviewed by Dugatkin, 1997), rodents (Rutte & Taborksy, 2008), birds (Krama et al., 2012; Krams, Krama, Igaune, & Mänd, 2008; Krams et al., 2013), and primates (reviewed by de Waal & Suchak, 2010; Schino & Aureli 2008, 2009). As a consequence, theorists attempt to explain why reciprocity is so rare (André, 2014), while others view reciprocity as an important and underappreciated mechanism for cooperation (Schino & Aureli, 2010a,b; Taborsky, 2013).

Reciprocity assumes that cooperative investments can be exploited if the recipients do not provide adequate cooperative returns back to the actor (i.e., 'cheating' Ghoul, Griffin, & West, 2013), and it predicts that individuals will therefore adjust these investments contingent on the returns received from their partners. Some authors contrast 'direct reciprocity' (A helps B because B helps A) with 'indirect reciprocity' (A helps B because B helps C) or 'generalized reciprocity' (A helps B because A was helped), and some authors separate positive reciprocity (contingent reward) from negative reciprocity (contingent punishment). The tendency of humans to both cooperate and punish non-cooperators, even at a cost or in one-shot economic games, has been called 'strong reciprocity' (reviewed by West et al., 2007b, 2011). Here, I focus exclusively on 'direct reciprocity' and do not distinguish between positive and negative effects. Relevant terms are defined in Box 1.

Box 1. Glossary

Altruism: cooperation that on average decreases the actor's direct fitness.

Byproduct mutualism: mutual benefits that are incidental (the traits or behaviors were not shaped by natural selection to provide benefits to others).

Cooperation: a behavior or trait that on average increases the inclusive fitness of both the actor and the recipient; includes altruism and mutualism.

Cooperative investment: an action that aids a recipient and functions to provide a cooperative return to the actor.

Cooperative return: an action by a recipient of a cooperative investment that increases the investor's direct fitness.

Direct fitness: lifetime reproductive success; number of total offspring that survive until adulthood.

Enforcement mechanism: a behavior or ability that functions to ensure that cooperative investments yield an indirect or direct fitness return (enforcement prevents cheating).

Cheating: occurs when a cooperative investment decreases the helper's inclusive fitness (the recipients do not provide a cooperative return or are not the intended recipients).

Inclusive fitness: the sum of direct and indirect fitness (traits are adaptive when they increase inclusive fitness).

Indirect fitness: the component of inclusive fitness gained from helping relatives.

Mutualism: cooperation that on average increases the direct fitness of the actor and recipient.

Pseudoreciprocity: unconditional cooperative investments that enable an inevitable byproduct return (no cheating and no enforcement).

Reciprocity: contingent cooperative investments that are based on the cooperative returns (enforcement through partner control and/or partner choice).

The reciprocity controversy depends more on semantic disagreements than on disputes about observable behavior or social evolution theory. Whereas the original concept of reciprocity was broad (Axelrod & Hamilton, 1981; Trivers, 1971), operational definitions gradually diverged and became narrower in meaning, but these multiple definitions are now used interchangeably, resulting in confusion. Most studies of reciprocity have tested if the short-term payoffs of a given scenario in nature fit the Prisoner's Dilemma game structure and if the behavior of organisms follows the strategy "tit-for-tat" (cooperate, then copy partner's last move). This model of reciprocity has led to four problematic distinctions that have essentially defined 'reciprocity' out of existence. First, some animal behavior researchers have taken the play of economic games very literally and assume that reciprocity is an intentional strategy requiring an understanding of game payoffs and the ability to keep score, plan ahead, and delay gratification (I call this 'the calculated reciprocity error'). Second, some operational definitions focus exclusively on short-term contingency with a single partner while ignoring factors such as partner choice, power asymmetries, and foundations of prior experience ('the short-term contingency bias'). Third, some definitions require demonstrating that an adaptive helping behavior reduces lifetime fitness but only in the short-term ('the temporary fitness cost paradox'). Finally, endless controversy concerns whether the returns on a cooperative investment are costly and strategically enforced (reciprocity) or self-serving and inevitable (pseudoreciprocity), a distinction that can be semantic ('the byproduct ambiguity'). To understand how these issues have arisen, we must take a historical perspective.

Historical Background

Robert Trivers (1971) coined the term ‘reciprocal altruism’ to explain how apparently altruistic behavior could evolve between non-kin. ‘Reciprocal altruism’ is not a form of altruism in the evolutionary sense (*sensu* Hamilton, 1964) because it does not decrease lifetime direct fitness. Many authors therefore prefer the term ‘reciprocity’ (Alexander, 1974; Axelrod & Hamilton, 1981; West et al., 2007a,b). The choice of the term ‘reciprocal altruism’ has likely led to at least some of the confusion that reciprocity is an alternative to mutual benefit, rather than a way of enforcing it (West et al., 2007b).

Trivers (1971) defined ‘reciprocal altruism’ in both narrow and broad terms. In the narrowest sense, he described various ways that it could operate in humans. In the broadest sense, he considered almost any case of a delayed mutual benefit to support the theory. For example, he imagined a hypothetical scenario in which a bird benefits from alarm calling because the act somehow makes a predator less likely to target the caller in the future. In his description, any social benefit to other birds was an incidental byproduct, a form of cooperation now called byproduct mutualism (Brown, 1983; Connor, 1986, 1995a; West-Eberhard, 1975). Modern usage of the term reciprocity excludes simple byproduct mutualisms, and Trivers (2006) later clarified this point himself.

Axelrod and Hamilton (1981) modeled reciprocity using the simple strategy “tit for tat” in the repeated Prisoner’s Dilemma. In this game, each player chooses to ‘cooperate’ or ‘defect’ and receives a different payoff depending on the other’s simultaneous response. Four payoffs are possible: both players cooperate (R, reward for mutual cooperation), cooperate with defector (S, sucker's payoff), defect against cooperator (T, temptation to defect), or both players defect (P, punishment for mutual defection). In the single-shot Prisoner's Dilemma, $T > R > P > S$, and defection is the only stable strategy. If the game is repeated in a series of continual rounds, then "tit for tat" (cooperate on first round, then copy player's last move) can outcompete "always defect" and many other strategies.

This model led to an explosion of subsequent game theory models for cooperation. Reciprocity was soon equated with both game theory and tit for tat. Yet it was still unclear exactly what constituted empirical evidence for reciprocity and how best to translate game theory to experiment. The ambiguity in defining reciprocity led to a workshop meeting where leading researchers concluded that reciprocity "might be very rare and restricted to a few groups, or it might be quite common and widespread – this depends on how the phenomenon is defined and the importance attributed to animals' intentions" (Taylor & McGuire, 1988, p. 69). Axelrod and Hamilton (1981) considered reciprocity broadly applicable to cooperation between neighboring male songbirds, interspecific mutualisms, microbes, viruses, and even chromosomes.

Several authors argued that the original definition of reciprocity was too broad (e.g., Koenig, 1988; Waltz 1981). These researchers thought the term had become too inclusive, because behaviors such as monogamy (Ligon 1983), mutual restraint of aggression (Lombardo, 1985), and sex (West-Eberhard, 1975) were being labeled as reciprocal altruism or reciprocity. In response, they argued that 'reciprocal altruism' should be used only for acts of helping that pose fitness costs to the helper (Koenig, 1988; Wilkinson, 1988).

By the 1990s, some reviews claimed that reciprocity was common (e.g., Dugatkin, 1997) while others argued that it was rare (e.g., Clements & Stephens, 1995). In most cases, the controversy involved whether a particular behavior actually conforms to tit-for-tat in the Prisoner's Dilemma (reviewed by Noë, 2006; Pusey & Packer, 1997; Raihani & Bshary, 2011). By the mid-2000s, interest in the Prisoner's Dilemma game as a model for cooperation had begun to decline due to the difficulty in translating theory to reality (Noë, 2006, Raihani & Bshary, 2011). Trivers (2006) lamented that:

> *Theorists and empiricists alike were forgetting that iterated games of PD amount to a highly artificial model of social interactions; each successive interaction simultaneous, costs and benefits never varying, options limited to only two moves, no errors, no escalated punishment, no population variability within traits and so on. In fact, almost all of these simplifying assumptions have now been shown to introduce important effects.* (p. 70).

As game-theoretical models grew increasingly detached from empirical work (e.g., Nowak, 2006), the term reciprocity, now associated with such models, fell out of favor with behavioral ecologists. As expressed by West et al. (2007a):

> *We do not need more convoluted theoretical analyses of games such as the Prisoner's Dilemma, snow drift, etc. … games such as the Prisoner's Dilemma and its solution with various forms of reciprocity make a large number of extremely specific and often unrealistic assumptions.* (p. R669).

Yet at the same time, work on interspecific mutualisms was accumulating a great deal of evidence that cooperative investments are indeed contingent on variable cooperative returns (Box 2). But the term 'reciprocity' was rarely used here. Instead, researchers referred to 'sanctions' (Kiers, Rosseau, West, & Denison, 2003), 'reciprocal rewards' (Kiers et al., 2011), and 'partner choice' (Noë & Hammerstein, 2001). Reciprocity is now largely equated with intraspecific, rather than interspecific cooperation even though it was applied originally to both (Axelrod & Hamilton, 1981; Trivers, 1971).

Experimental studies on cooperative exchanges among fish, plants, fungi and bacteria have tested the behavioral response to simulated cheating by making one partner able to receive, but not reciprocate, a cooperative investment (e.g., Kiers et al., 2003, 2011). The results of such studies have shown that partner choice, partner switching, and partner control (reward and punishment of a single partner), as well as various byproduct benefits that depend on ecological circumstances, can all play key roles in stabilizing cooperation (Box 2). These results clearly illustrate that enforcement mechanisms are often necessary to stabilize cooperation and complex cognition is not required for sophisticated mechanisms of partner control or choice.

Such studies also demonstrated the utility of viewing cooperation using the metaphor of investment, exchange, supply, and demand. This approach was developed by biological market theory (Noë & Hammerstein, 1994, 1995, 2001) and has provided some of the clearest predictions regarding cooperation both between and within species (e.g., Fruteau, Voelkl, Van Damme, & Noë, 2009; Kiers et al., 2011). Biological market models have now largely replaced the prisoner's dilemma and other game theory models for guiding empirical studies of what used to be described as reciprocity.

Box 2. Examples of contingent cooperative exchanges in intraspecific mutualisms

In the cleaner-client fish mutualism, small cleaners cooperatively eat dead skin off larger ‘client’ fish, but can also ‘cheat’ by eating mucus or live tissue (Grutter, 1999). Both cleaners and clients enforce cooperation. Clients abandon or punish cleaners that cheat and avoid cleaners that they observe cheating (Bshary & Grutter, 2002a, 2005, 2006). Cleaners remember the time, location, and quality of client interactions (Salwiczek & Bshary, 2011), behave more cooperatively when observed by non-resident clients (Bshary & Grutter, 2006, Pinto, Oates, Grutter, & Bshary, 2011), increase cooperation by punishing other cleaners (Bshary, Grutter, Willemer, & Leimar, 2008, Raihani, Grutter, & Bshary, 2010), and adjust the extent of third-party punishment to client value and the size of conspecific partners (Raihani, Pinto, Grutter, Wismer, & Bshary, 2012).

Plants exchange resources with several symbiotic partners, including mycorrhizal fungi, rhizobia bacteria, and pollinating insects. By diverting resources to different structures, plants selectively kill symbionts that do not provide returns ('sanctions', Kiers et al., 2003; see also Goto, Okamoto, Toby Kiers, Kawakita, & Kato, 2010; Jandér & Herre, 2010). In other cases, contingent enforcement is reciprocal; in the plant-mycorrhizal fungi mutualism, both partners reward high returns and punish low returns (Hammer, Pallon, Wallander, & Olsson, 2011; Kiers et al., 2011). Importantly, the contingent investments are often continuous rather than discrete such that the intensity of sanctions matches the amount of the return (Kiers, Rosseau, & Denison, 2006).

In the acacia-ant mutualism, a host plant exchanges nectar for defense by ants. Even before enforcement is considered, cheating is already inhibited by a byproduct benefit; the aggressiveness of ants is linked to both their ability to defend host plants and to outcompete less aggressive ant species (Heil, 2013). However, plants still possess several enforcement strategies. They produce nectars that are difficult to digest for non-mutualists (Orona-Tamayo et al., 2013), and these nectars also manipulate the digestive system of their ant mutualists towards dependency on the nectar rewards (Heil, Barajas-Barron, Orona-Tamayo, Wielsch, & Svatos, 2103). On the other end, ant strategies of partner control appear to include contingent defense of plants based on amount of nectar supplied (Orona-Tamayo & Heil, 2013).

The Calculated Reciprocity Error

Recent authors have argued that reciprocity requires sophisticated cognitive abilities for making planned intentional investments with an expectation of a future reward (e.g., Hauser, McAuliffe, & Blake, 2009; Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2006; Russell & Wright, 2009; Stevens, Cushman, & Hauser, 2005; Stevens & Hauser, 2004). For example, Stevens and Hauser (2004) stress that reciprocity is potentially limited by capacities for "numerical discrimination, time estimation, delayed gratification, detection and punishment of cheaters, analysis and recall of reputation, and inhibitory control." This 'calculated reciprocity' (de Waal & Luttrell, 1988) leads to an operational definition that requires testing that an animal can strategically resist the temptation to defect to obtain a delayed social reward, even under extremely artificial conditions. For instance, experiments found that blue jays did not learn to perform a tit for tat strategy in an operant conditioning paradigm that mimicked a Prisoner's Dilemma in the absence of any natural or social cues (Clements & Stephens, 1995; Stephens, McLinn, & Stevens, 2002, reviewed by Noë, 2006). Evidence for calculated reciprocity in nonhuman animals under these conditions is rare (e.g., Hauser et al., 2009, but see Dufour, Pelé, Neumann, Thierry, & Call, 2009). This evidence has been used to suggest that reciprocity might be rare in nature, but this conclusion assumes that all reciprocity is calculated reciprocity and acquired through associative learning.

The alternative view is that the 'calculations' required for reciprocity occur not via associative learning alone, but through task-specific adaptations, which require the proper ecologically relevant cues to act as triggers. According to this view, reciprocity occurs as a species-specific cognitive specialization similar to evolved mechanisms for mate choice, navigation, or kin recognition. For example, the extraordinary species-specific abilities of food-caching birds to remember thousands of cache locations over months is not constrained by the supposed difficulties of long-term memory, delaying gratification, and planning for the future (Bednekoff, Balda, Kamil, & Hile, 1997).

With this in mind, Stevens et al. (2005) acknowledged that "we should expect to find reciprocity and punishment in instances where adaptation has overcome the initial cognitive constraints – where narrowly tailored cognitive mechanisms have evolved to support specific behavioral routines (p. 512)." The controversy over the cognitive constraints on reciprocity therefore rests on deeper controversies over how easily adaptation overcomes cognitive constraints and how often social behaviors rely on context-specific adaptive specializations rather than on associative learning (e.g., Magphail & Bolhuis, 2001).

An adaptationist view is that associative learning cannot fully explain reciprocity. Consider that kin discrimination (which is often based on prior association) requires different adaptive designs for different taxa. This results not only from physical constraints (e.g., plants don't have brains), but also differing ecological requirements (e.g., location-based offspring recognition can work for stationary bank swallow nestlings but not mobile penguin chicks). Even when reciprocity is based on learning the relative payoffs of helping through operant conditioning, this learning process will likely be shaped by natural selection, such that the task will be acquired faster in species performing reciprocity. This prediction is consistent with the finding that adult cleaner fish outperform juvenile cleaners and several primates at learning a cooperative task that simulates the payoffs that cleaners regularly face in nature (Salwiczek et al., 2012).

Calculated reciprocity in humans.

Even in humans, calculated reciprocity in humans often appears ‘instinctive’, subconscious, and context-specific. Rather than relying on strategic self-control, many human prosocial behaviors are fast, intuitive, and built into our basic emotions (Frank, 1988; Trivers, 1971). Reasoning through a logic puzzle is slow and difficult compared to the way insight is quickly gained about the same logical problem framed as a social exchange (e.g., Cosmides, 1989; Cosmides & Tooby, 1992). Testing calculated reciprocity-- by placing people in Prisoner’s Dilemma or other economic games—often leads to irrational decisions which appear to reflect decisions that would be optimal under more natural circumstances (Burton-Chellew & West, 2012, 2013). Humans treat single-shot economic games as if they might be repeated (Delton, Krasnow, Cosmides, & Tooby, 2011). Cooperative outcomes in the Prisoner’s Dilemma are inherently more rewarding and activate distinct reward regions in the brain when the payoffs occur with a human partner rather than with a computer (Abric & Kahan, 1972; Rilling et al., 2002). In stark contrast to avoiding a temptation to defect, most defectors feel an initial impulse to cooperate (Rand, Greene, & Nowak, 2012). Cooperative decisions to donate to public goods are influenced by irrational audience cues (e.g., pictures of eyes, Bateson, Nettle, & Roberts, 2006; Haley & Fessler, 2005) or cues to group competition (Burton-Chellew & West, 2012). Such findings only make sense if many heuristics for cooperative decision-making subconsciously rely on cues that would have maximized inclusive fitness in ancestral environments. In short, the payoffs as given by an experiment are not always the payoffs that are perceived by animal minds.

Similarly, social birds and mammals probably engage different neurocognitive mechanisms when learning that food can be obtained by grooming others versus pecking keys. The importance of ecological and social cues is therefore extremely relevant for reciprocity tests in both human and animal subjects. This likely explains why reciprocity experiments in nonhuman primates are more likely to find evidence for short-term contingency when the experimenters test natural helping behaviors in a group setting rather than use artificial designs with paired subjects performing instrumental tasks (Jaeggi, De Groot, Stevens, & Van Schaik, 2012).

The Short-term Contingency Bias

There is abundant and growing evidence for symmetrical patterns of helping at the group level (‘symmetry-based reciprocity,’ de Waal & Luttrell, 1988), which are consistent with reciprocity but not by kinship biases (e.g., bats: Wilkinson 1984, Carter & Wilkinson, 2013a,b,c; corvids: Fraser & Bugnyar, 2012; Scheid et al., 2008; primates: Gomes, Mundry, & Boesch, 2009; Schino & Aureli, 2008). However, such correlations tell us little about causation.

Experimental studies have historically emphasized short-term alternation of helping acts with a single partner, especially in primates (reviewed by de Waal & Brosnan, 2006; de Waal & Suchak, 2010; Schino & Aureli, 2009). For example, ‘attitudinal reciprocity’ (de Waal, 2000), relies on emotional scorekeeping, but is defined as when “parties mirror each other’s social attitudes with a high degree of short-term contingency” (de Waal & Suchak, 2010). However, an overemphasis on short-term alternating exchange can ignore the roles of prior long-term social relationships and partner choice.

Contingency in a human friendship.

Studies of how reciprocity works in humans can guide our expectations about what to expect in other primates or vertebrates. Whereas calculated reciprocity is used in human trade, most human social relationships (e.g. communal relationships, Clark & Mills, 1979) are likely enforced by attitudinal reciprocity. Trivers (1971) used reciprocity to explain friendship and moral emotions such as guilt, shame, gratitude, sympathy, and trust. But subsequent authors (e.g., Silk, 2003) have suggested that reciprocity cannot explain friendship because friends do not appear to closely track favors (the calculated reciprocity error). Humans express a stronger obligation to repay favors to strangers, while exchanges of goods or services in human friendships are often implicit, delayed, imprecise, and even offensive and taboo if they are explicit (Boster, Rodriguez, Cruz, & Marshall, 1995; Shackelford & Buss, 1996; Silk 2003). Why might this be?

One explanation is that a desire to immediately repay social debt signals that future interactions are not expected. Concealing expectations of ‘exchange’ might also function similarly to indirect speech (Pinker, Nowak, & Lee, 2008): it allows people to negotiate topics of implicit social conflict while maintaining plausible deniability about their own expectations. Put differently, friends do not discuss long-term exchange of social support services for the same reason that dating does not involve explicit discussion of reproduction.

Although often implicit, reciprocity is clearly embedded within the psychology of human friendships; social investments are affected by changes in the ability of friends to reciprocate, the availability of alternative friends, and the need for social support (e.g., Cosmides & Tooby, 1992; Frank, 1988; Shackelford & Buss, 1996; Tooby & Cosmides, 1996). Humans tolerate short-term imbalances with friends more than strangers and track the cooperative acts of strangers more than friends, but they still track the investments of friends (Xue & Silk, 2012). The same can likely be said for other kinds of social relationships such as between spouses or siblings.

Contingency in a long-term animal relationship.

Many nonhuman animals possess long-term cooperative social bonds that are functionally analogous to human friendships. Such long-term cooperative social bonds (henceforth "social bonds") are well described in chimpanzees and baboons (Seyfarth & Cheney, 2012), and there is also evidence for their existence in macaques, capuchin monkeys, elephants, feral horses, hyena, dolphins, bats, corvids, and mice (Braun & Bugnyar, 2012; Carter & Wilkinson, 2013c; Fraser & Bugnyar, 2012; Seyfarth & Cheney, 2012; Weidt, Hofmann, König, 2008; Weidt, Lindholm, & König, 2014). Field studies have demonstrated that strong social bonds provide clear fitness benefits (e.g., Cameron, Setsaas, & Linklater, 2009; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk et al., 2010).

Long-term social bonds are often better than recent social experience at predicting cooperative investments (Carter & Wilkinson, 2013a,c; Gomes & Boesch, 2011; Sabbatini, Vizioli, Visalberghi, & Schino, 2012; Seyfarth & Cheney, 2012). Partner fidelity through social bonding reduces social risks and facilitates the exchange of multiple cooperative investments such as information transfer, social thermoregulation and grooming, cooperative foraging and food sharing, and protection from predators and hostile conspecifics. Several primatologists have recently outlined how implicit knowledge of social relationships can simplify the process of reciprocity by reducing these multiple currencies of help into a single trackable currency of relationship quality (de Waal, 2000; Jaeggi et al., 2012; Massen, Sterck, & de Vos 2010; Schino & Aureli, 2009, 2010a,b; Seyfarth & Cheney, 2012; Tooby & Cosmides, 2008). For example, chimpanzees of both sexes appear to exchange several different commodities, including grooming, sex, support, and food, resulting in balanced long-term relationships (Gomes & Boesch, 2011). As Seyfarth & Cheney (2012) explained, “grooming on Tuesday can create an emotional bond that causes meat sharing on Saturday afternoon” (p. 167).

Similar to humans, nonhuman primates cooperate in a more contingent manner with *less* bonded partners (de Waal, 1997; Seyfarth & Cheney, 1984, 2012). Most experimental evidence for short-term contingencies comes from cooperation outside of social bonds (see below), which is consistent with the expected difficulty of altering a long-term social bond in a short window of time (Brosnan et al., 2009; Melis, Hare, & Tomasello, 2008). When Melis et al. (2008) found no clear evidence of contingency in two reciprocity experiments with captive chimpanzees, pre-existing social bonds may have been a confounding factor, because one particular chimp would always pull for a specific partner. One lesson here is that experiments on partner control should either use previously unfamiliar subjects or somehow account for the history of past interaction. This is especially important in the absence of partner choice, discussed below.

Contingency through partner choice.

Although some authors consider partner choice as a specific mechanism for reciprocity (Schino & Aureli, 2009, 2010a,b), reciprocity is typically equated with partner control (increasing and decreasing investment in a single partner) as opposed to partner choice (Noë & Hammerstein, 2001). However, Trivers (1971) recognized partner choice as a form of reciprocity stating that individuals could reciprocate by "decreasing to a minimum the possible exchanges between himself and a subtle cheater and replacing these with exchanges between a new partner or partners. In short, he can switch friends" (p. 47).

Partner choice is particularly relevant when some individuals have greater access to resources or a greater ability to provide services, increasing their value as social partners. In a particularly persuasive demonstration, Fruteau et al. (2009) manipulated the value of low-ranking wild vervet monkeys and observed the response of social partners. A single low-ranking female was given the ability to open a food cache for her entire social group, which led to an immediate spike in her grooming ratio (grooming received minus given). When a second low-ranking female was chosen to be an additional food provider, her grooming ratio spiked as well, and the first provider's grooming ratio decreased by roughly half (Fruteau et al., 2009).

Sabbatini et al. (2012) conducted tests of passive food sharing (tolerated theft) in capuchin monkey dyads (partner choice absent) and triads (partner choice allowed). In dyadic tests, food shared from A to B predicted food shared from B to A. In triadic tests, the within-dyad contingency was weaker and food sharing was predicted best by relationship quality, indicating that prior social bonds are more important than recent past sharing within a dyad. When cooperatively nursing female mice are allowed to choose preferred partners rather than non-preferred partners, they achieve higher direct fitness and more egalitarian reproductive outcomes (Koenig, 1994, 2006; Weidt et al., 2008, 2014).

Experimental evidence for short-term contingency.

Short-term contingency and partner choice are not alternatives; many reciprocity experiments testing short-term contingency use a partner choice design. Rutte and Taborsky (2008) trained rats to pull a lever to deliver food to conspecifics, and found that rats were more likely to pull for partners that previously pulled for them. Anonymous help increased pulling by 20% and help from the same partner increased it an additional 51% (Rutte & Taborsky 2008).

Under natural conditions, short-term contingency should be most obvious in scenarios where partner choice is reduced or absent. Examples include male songbirds on neighboring territories (discussed below under "temporary fitness cost paradox") or mated pairs raising offspring together. Great Tit parents were found to feed nestlings in a balanced alternating pattern unexplainable by foraging or begging times. Each parent increased feeding rates after their partners contributed, but reduced their feeding rate by about 25% until their partner contributed (Johnstone et al., 2014).

Experimental evidence of reciprocity comes from mobbing behavior of birds. Krams et al. (2008) used fake owls to induce cooperative mobbing in 44 triads of pied flycatcher mated pairs, with each triad consisting of three equidistant nestboxes (A, B, and C). Pair A was exposed to a fake owl near their nestbox to induce mobbing, pair B was held captive and prevented from mobbing, and pair C was left untreated, such that pair C always helped pair A with mobbing, but pair B could not. The authors then simultaneously presented pairs B and C with owls, and tested at which nestbox pair A would choose to help. In 30 of 32 trials, pair A helped pair C. In a follow-up experiment, pair B was presented with an owl. In 8 of 9 trials, pair C, but not pair A, joined B in mobbing, as expected if mobbing efforts are reciprocated in a contingent manner.

Like most claims of reciprocity, this conclusion has been strongly disputed. Russell and Wright (2009) implied that reciprocity was too cognitively difficult for this species (the calculated reciprocity error), and did not consider the form of helping to be costly (see ‘the temporary fitness cost paradox’ below and Wheatcroft & Krams, 2009). Connor (2010) suggested that pair A did not help pair B in order to avoid a potential parasite infestation. These alternative hypothesis seem to assume that reciprocity is highly unlikely *a priori*.

Krama et al. (2012) ruled out the possibility that reciprocal mobbing at nestboxes was purely a byproduct benefit by showing that the degree of contingency was dependent on the costs and benefits. In the original study, nestboxes were 48-54 m apart. At closer distances (20-24 m apart), they found that subjects always helped neighbors mob regardless of past defections. At farther distances (69-84 m), the original finding was again replicated: pairs helped neighboring pairs contingent on prior help. When the predator was nearby and benefits of mobbing were very high, it was always worth mobbing and any benefit to others was incidental and not enforced. When the predator was farther away, the mobbing was more of a cooperative investment enforced by reciprocity. Hence, reciprocity can involve both byproduct benefits and enforced benefits with their relative importance determined by circumstances.

The degree of reciprocity was also sensitive to whether the failure of partners to mob was caused by their absence ("the excuse principle" Krams et al., 2013). To simulate voluntary defection, the experimenters removed pair B, but played pair B alarm calls to simulate their presence. To simulate involuntary absence, the experimenters completely removed pair B during the predator presentation. When pair B birds appeared present but unwilling to join, pair A only helped pair B in only 2 of 20 cases, but when pair B was completely absent, pair A helped the mob in 20 of 21 cases.

The Temporary Fitness Cost Paradox

Clutton-Brock (2009) argued that no putative case of reciprocity has demonstrated that "assistance has a net fitness cost at the time it is provided" (p. 54). This is an extremely difficult, if not impossible, demonstration given that opportunity costs, energetic costs, and increased mortality risk (e.g., predator inspection by small fish: Milinski, Lüthi, Eggler, & Parker, 1997; food sharing in vampire bats: Wilkinson, 1984) have been considered insufficient evidence (Clutton-Brock, 2009;

Pusey & Packer, 1997). This temporary fitness costs paradox stems from the fact that many authors including Trivers (1971) define altruism based on short-term payoffs rather than lifetime fitness costs. Although this definition is closer to popular usage, it has led to much confusion in the social evolution literature (West et al., 2007b).

The temporary fitness cost paradox is equivalent to saying that reciprocity assumes that helping others poses a risk, the possibility of cheating, even though the consequence of reciprocity is to prevent cheating. In other words, demonstrating reciprocity requires showing that it doesn't perform its function. This paradox is rooted in a deeper problem regarding the notion of byproducts and inevitable returns (see 'the byproduct ambiguity' below).

One point of the temporary cost requirement is to exclude behaviors that are not forms of helping. For example, several authors have viewed mutual restraint among neighboring male songbirds as reciprocity (Akçay et al., 2009; Axelrod & Hamilton, 1981; Getty, 1987; Godard, 1993; Hyman, 2002). As male songbirds on neighboring territories become familiar they tend to reduce territorial defense and vocal aggression towards one another as compared to strangers ('the Dear Enemy effect'). Playback studies simulating territorial intrusions by neighboring males found that male hooded warblers increased vocal aggression after playback of those same neighbors compared to control playbacks of other males (Godard, 1993). In similar playback tests, male song sparrows increased their vocal retaliation to previously intruding neighbors but not to others (Akçay et al., 2009). Male red-winged blackbirds did not demonstrate the Dear Enemy effect given that they were more aggressive to neighbors than to strangers, but they did appear to contingently retaliate against neighbors based on their past actions (Olendorf, Getty, & Scribner, 2004).

Is it fair to call this contingent restraint ‘reciprocity’? Some argue that restraint is not ‘costly’ enough (e.g., Koenig, 1988), but such distinctions are semantic. Fitness costs and benefits are always relative to possible options. When an animal allows only some individuals to use a burrow, feed at a carcass, or take food from its hand, this can be seen equivalently as either conditional punishment or reward. Arguments about whether the Dear Enemy effect should ‘count’ as reciprocity just detract from more important points, for instance, that enforcement of mutual benefit by short-term contingency differs by species, does not require sophisticated cognition, and might be more clear when partner choice is limited by natural circumstances.

The Byproduct Ambiguity

Reciprocity involves mutual enforcement though cooperative investments contingent on cooperative returns. By contrast, ‘pseudoreciprocity’ does not require enforcement because cooperative investments simply *enable* inevitable byproduct returns (Bergmüller, Johnstone, Russell, & Bshary, 2007; Bshary, 2010; Connor, 1995a, 2010). Pseudoreciprocity assumes that the returns are self-serving byproducts and hence bestowed automatically. Whereas reciprocity involves symmetrical investments, pseudoreciprocity is inherently asymmetrical because it assumes that only one partner makes an investment. Pseudoreciprocity and other byproduct models have been posed as more plausible alternative explanations for almost all putative cases of reciprocity (e.g., Bshary, 2010; Connor, 2010; Raihani & Bshary, 2011). Despite the purportedly clear theoretical distinctions, it is often unclear both how to classify real cases, and why it would be useful to do so. As an illustration, consider one of the most contested claims of reciprocity - predator inspection in fish.

Predator inspection in fish: A case study of byproduct ambiguity.

Pairs of fish sometimes approach and inspect larger predatory fish, presumably to assess the situation while maintaining the safety of a companion. The reciprocity explanation claims that fish enforce partner cooperation by approaching closer only if the partner swims beside them (Milinski, 1987). Evidence suggests that predator approach behavior is riskier for both single fish (Pitcher, Green, & Magurran, 1986) and leading fish (Milinski et al., 1997). Predator inspection involves partner recognition and is contingent on a partner's past and present predator inspection behavior (Dugatkin, 1988, 1997; Dugatkin & Alfieri, 1991; Milinski, 1987; Milinski, David, & Kettler, 1990), and is more likely to occur with particular partners that have histories of other past social interactions (Croft et al., 2006). Differences in predator inspection behavior of fish from habitats with either high or low predation suggest that the behavior has been shaped by natural selection (Dugatkin & Alfieri, 1992).

Like the similar mobbing behavior in pied flycatchers, this claim of reciprocity has attracted much criticism. One alternative byproduct model argued that the "two individuals jointly adopt the same actions they would perform if alone" (Stephens, Anderson, & Benson, 1997, p. 130), and some authors argued that the movements result even in the absence of a predator (Masters & Waite, 1990; Stephens et al., 1997). Therefore, the supposed cooperation actually resulted from “the simple statistical combination of individual orientation to a predator and attraction to a companion” (Stephens et al., 1997, p. 129). However, other studies using different species present contradicting evidence that inspection is indeed contingent on the existence of a predator (Dugatkin, 1991). Moreover, the observation that fish have preferred inspection partners (Croft et al., 2006; Dugatkin & Alfieri, 1991; Dugatkin, 1997, Milinski et al., 1990) cannot be reconciled with a simple model that assumes no social interactions.

A more nuanced byproduct explanation assumed preference for previously bold individuals, consistent partner choice, and the idea that fish remembering a specific partner “could ‘trust’ it to be bold during subsequent interactions” (Connor, 1996, p. 453). The difference between partner choice for fish that are ‘bold’ versus ‘cooperative’ is admittedly semantic (Connor 1996), and the distinction between this byproduct and reciprocity model is based not on the decisions of the fish but on different interpretations of the costs and benefits. For example, the payoff matrix for leading and lagging behind might not match a Prisoner’s Dilemma but rather a Hawk-Dove Game (also called Snowdrift or Chicken Game), such that bold leaders (dove) do better with other bold leaders but it will still pay to boldly lead with a parasitic laggard (hawk) because two laggards do worst of all (Noë, 2006). According to Connor (1996) and Stephens et al. (1997), this would mean the behavior is not reciprocity. As Stephens et al. (1997) summarized, “the only unambiguous way to distinguish between competing economic models of predator approach is by objective measurement of the economics (i.e. the payoff matrices).” The assumption is that, to understand the behavior, it must be classified as a strategy in a particular game.

The problem is that predator inspection actually looks less like any particular game the more one examines it (Noë, 2006). Fish are not choosing between binary options, such as leading or lagging; rather, they can approach to varying distances at varying speeds. Depending on information about the partner, the actor, and the circumstances, the costs and benefits of leading or lagging can be adjusted continuously by leading ahead a bit less (‘parceling’ Connor, 1995b) or a bit more (‘raising the stakes’ Roberts & Sherratt, 1998). For example, the contingency of mobbing decisions by pied flycatchers varies with predator distance, because the perceived payoffs change with perceived risks (Krama et al., 2012). Views on how well biological reality matches a particular game depend on how literally one takes the game assumptions, how one divides the cooperative behavior into rounds, and how one assigns behavior to the binary choices. For these reasons, debates regarding how well various natural behaviors match the Prisoner’s Dilemma are typically not resolved by additional empirical evidence (Clements & Stephens, 1995; Doebeli & Hauert, 2005; Dugatkin, 1997; Milinski et al., 1997; Noë, 2006; Pusey & Packer, 1997; Raihani & Bshary, 2011; Stephens et al., 1997).

Game payoffs and the byproduct ambiguity.

Game theory payoff structures and their outcome in evolutionary simulations are drastically altered when allowing any additional element of realism such as kinship, spatial structure, partner switching, communication, long-term relationships, power asymmetries, and continuous variation in the size of cooperative investments

(Doebeli & Hauert, 2005; Noë, 2006). Payoffs for partners in the real world might also be asymmetric, so each individual or type of individual would in effect be playing a different game. Consider a scenario where some lions can lead the rush to protect a territory from intruders or lag behind and get the benefits of defense without paying the costs (Connor, 2010; Doebeli & Hauert, 2005; Heinsohn & Packer, 1995). Territory defense might be a Hawk-Dove Game for male lions because they can lose all their offspring if ousted by a foreign male (leading alone > mutual defection). Whereas for female lions the same scenario might be closer to a Prisoner's Dilemma (mutual defection > leading alone) because they are likely to sacrifice some, but not all, of their reproductive success if the foreign male gains control. In this case, are male lions performing pseudoreciprocity, while female lions are performing reciprocity?

Strategic adaptive behaviors are always reducible to a combination of very simple decision rules, which are themselves byproducts of other adaptations. So if joint predator inspection in fish is shown to be merely based on a foundation of simple byproduct behaviors, this demonstration of how the contingency works does not refute the idea that decisions of fish are enforced by that contingency. The fact that fish benefit from preferentially choosing bold leaders as partners is already enough contingent aid to help enforce cooperation. Partner choice already assumes that fish are keeping track of their partners' actions and identity, so why would they not use this information to also guide their actions within dyads?

Byproduct explanations are not favored because they are empirically verified; rather they usually act as null hypotheses. Moreover, they explain behaviors already known to exist, rather than make new predictions of what animals should do to maximize fitness. For example, in a review arguing for the absence of evidence for reciprocity, Clutton-Brock (2009) suggested that simple byproducts or pseudoreciprocity could explain elements of mutualism or manipulation such as:

> *Regularly associating with dominant individuals, and grooming them repeatedly [in order to] habituate them [and gain] shelter from competition" as well as the "establishment and maintenance of long-term mutualistic relationships…[in which] individuals compete to establish relationships with potential protectors, allies or mates, using a wide range of different forms of affiliative behavior, including close association, grooming, support in competitive interactions, reassurance, and consolation.* (p. 55).

In all these cases, the individuals are not reciprocating; rather they *merely* "modify their behavior to take advantage of the fixed responses of conspecifics." But if such relationships are completely explained by simple byproduct benefits and do not require enforcement, why then do such complex, long-term social relationships correlate with brain size (Dunbar & Shultz, 2007, 2010)?

In many cases, classifying cases as reciprocity or pseudoreciprocity is more clearly semantic. Reciprocal egg-trading by hermaphroditic fish involves the alternated exchange of valuable eggs for fertilization by the partner (Fischer, 1984; Sella, 1985). The reciprocity explanation has been contested using an alternative byproduct model by Connor (1992) who acknowledges that such egg trading represents a costly investment leading to a costly return and that individuals “parcel those benefits to manipulate each other’s optimal strategy” while also arguing that, “in reciprocity, an individual would realize short-term benefits by cheating on any given interaction. This is not the case in the model presented here” (p. 523). Again, this is a semantic distinction, which depends on how one divides behavior into ‘interactions’. A crucial question is whether the reciprocity hypothesis can ever produce testable predictions that cannot be later explained as consistent with a byproduct explanation.

Byproduct benefits and enforced benefits are not mutually exclusive. Indeed, most enforced benefits likely originated as byproduct benefits, because the frequency of cheating can fluctuate in a population such that a given benefit might be considered ‘a fixed response’ or not, depending on the phenotypes currently in the population. When a cooperative trait goes to fixation, this eliminates the selective pressure for enforcement mechanisms such as contingency. Eventually the trait can become unconditional and hence susceptible again to cheating, which can easily arise again from new variation in the cooperative trait (Foster & Kokko, 2006; Imhof, Fudenberg, & Nowak, 2005).

The line between different kinds of byproduct mutualism and pseudoreciprocity can also be subjective. Raihini & Bshary (2011) explain that seed dispersal is either byproduct mutualism or pseudoreciprocity depending on which organism’s perspective is taken:

> *The plant invests resources into making seeds that are attractive to some animals. This enables a self-serving response from the animal that eats the seed and later disperses it via defecation. Because the plant makes an initial investment in the interaction, but there is no potential to benefit from reducing this investment, we can explain the plant's investment with the concept of positive pseudo-reciprocity. The animal, on the other hand, simply eats the seed and later defecates: there is no investment and the benefits to the plant are a by-product of the animal's own self-serving behavior.* (p. 1635)

The authors assume that there is no potential benefit for a plant to reduce its investment, but this is only because the fitness of a plant that produces poor fruits would be reduced by partner choice. If a particular fruit tree provides poor fruit, animal foragers stay away. This is because animals make a costly investment in selecting fruits to open, eat, or carry away. From the plant's perspective, the cooperative returns (seed dispersal) are thus not fixed, but depend on the size of the investment (fruit quantity and quality). From the animal's perspective, the cooperative returns (fruit quality) might depend on the cooperative investment (choosing to move to one fruit tree over another). Here, we see that the line between byproducts and enforced benefits is blurred further.

Defining Reciprocity

Evolutionary explanations of cooperation are drawn from several academic sub-fields, leading to many semantic misunderstandings and disagreements (West et al., 2007b). The semantic framework one chooses ultimately depends on what is most useful. But for authors discussing reciprocity, it will be particularly important to define their terms, because reciprocity has many different contradictory meanings in the literature. In this review, I defined reciprocity as occurring when individuals make contingent cooperative investments based on past or expected returns. I believe that this simple, testable definition best captures the original broad concept described by Trivers (1971) and Axelrod and Hamilton (1981). Under this definition, reciprocity is a broad overarching term for conditional enforcement of direct fitness cooperation, including sanctions (Denison, 2000; Kiers et al., 2003; West, Kiers, Simms, & Denison, 2002), reciprocal rewards (Kiers et al., 2011), partner control, and partner choice (Foster & Wenseleers, 2006; Noë & Hammerstein, 2001).

Conclusion

Three key theoretical frameworks have guided empirical studies of cooperation. Inclusive fitness theory (Hamilton, 1964) solved the puzzle of altruism. Reciprocity theory (Axelrod & Hamilton, 1981; Trivers, 1971) illustrated the roles of contingency and frequency-dependent selection in cooperation. Biological market theory (Noë & Hammerstein, 1994) clarified the importance of partner choice and asymmetries in exchange rates. Unfortunately, several unnecessary controversies have resulted from incompatible modeling approaches and semantic frameworks that actually make the same predictions in the real world. One example is the social evolution debate regarding inclusive fitness and multi-level selection (or ‘kin selection versus group selection,’ see Marshall, 2011; West et al. 2007b). Similarly, reciprocity involves a number of competing semantic frameworks. These semantic differences can lead to disagreements about facts, when for example authors mistakenly believe that behaviors described as reciprocity (in a broad sense) are unlikely to be real or important, because reciprocity (in a narrow sense) is rare. Rather than subjectively fitting behaviors to a game metaphor, a broader notion of reciprocity allows researchers to focus on testing the relative importance of different social and ecological factors that influence helping behavior. Hopefully, this review will help distinguish real alternative hypotheses from semantic disagreements based on modeling preferences ("all models are wrong, but some are useful," Box & Draper, 1987, p. 424).

Cooperative traits cannot always be clearly classified as byproducts versus enforced, direct fitness versus indirect fitness, or altruistic versus mutualistic. Many cooperative behaviors, especially those in complex animal societies, are supported not by a singular mechanism, but rather by a complex interacting set of decision rules that take into account multiple factors such as genetic relatedness, partner choice, short-term returns, and long-term prior relationships (e.g., cooperative breeding in cichlids: Zöttl, Heg, Chervet, & Taborsky, 2013; food sharing in primates: Jaeggi & Gurven, 2013; Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013; food sharing in vampire bats: Carter & Wilkinson, 2013a).

How then should we classify various mechanisms (and should we even try to)? One proposal is to avoid the term reciprocity and simply refer to 'cooperative investments' and 'cooperative returns' (Noë 2006). However, simply abandoning the term 'reciprocity' cannot resolve past controversies or clarify connections between recent findings and older studies. In fact, using the terms ‘investment’ and ‘return' already assumes much of what reciprocity predicts— that helping another individual is a conditional investment leading to a return that is not fixed. Whatever this phenomenon is called, it is clearly important across many cooperative organisms with repeating interactions.

Acknowledgements

Jerry Wilkinson, Jennifer Vonk, and two anonymous reviewers provided comments that greatly improved the manuscript. GGC is supported by a Ford Foundation Predoctoral Fellowship administered by the National Academy of Sciences and his work on vampire bats is supported by the National Science Foundation under Grant No. (1311336).

Chapter 2: Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment

Abstract

Common vampire bats often regurgitate food to roost-mates that fail to feed. The original explanation for this costly helping behaviour invoked both direct and indirect fitness benefits. Several authors have since suggested that food sharing is maintained solely by indirect fitness because non-kin food sharing could have resulted from kin recognition errors, indiscriminate altruism within groups, or harassment. To test these alternatives, we examined predictors of food-sharing decisions under controlled conditions of mixed relatedness and equal familiarity. Over a 2-year period, we individually fasted 20 vampire bats (Desmodus rotundus) and induced food sharing on 48 days. Surprisingly, donors initiated food sharing more often than recipients, which is inconsistent with harassment. Food received was the best predictor of food given, and 8.5 times more important than relatedness. Sixty-four percent of dyads were unrelated, approaching the 67% expected if nepotism was absent. Consistent with social bonding, the food-sharing network was consistent and correlated with mutual allogrooming. Together with past work, these findings support the hypothesis that food sharing in vampire bats provides mutual direct fitness benefits, and is not explained solely by kin selection or harassment.

Introduction

Cooperation poses an evolutionary puzzle whenever a donor pays a cost to help a recipient: what prevents recipients from receiving the reproductive benefits of donor cooperation without paying the costs? Several mechanisms can prevent such 'cheating' thereby ensuring that cooperative investments yield net inclusive fitness benefits (West et al. 2007a). The exploitation of altruism is often prevented through kin discrimination (Griffin & West 2003) or policing (Ratnieks & Wenseleers 2008), whereas direct fitness cooperation can be enforced by behaviours that reward helpers, punish cheats, or both (Noë & Hammerstein 1994; Kiers et al. 2003, 2011; West et al. 2007a; Jander & Herre 2010, Fruteau et al. 2011). To identify what mechanisms enforce or maintain cooperation, controlled experiments can directly test how individuals respond to cheating. The most successful of such experiments involve organisms that are easy to manipulate in the lab (e.g. Grutter & Bshary 2003; Kiers et al. 2003, 2011; Bshary & Grutter 2005, 2006; Diggle et al. 2007). Studies using more cognitively complex organisms, like nonhuman primates, are often limited to learned behaviours, such as pulling levers to deliver food to others (e.g. Noë 2006, de Waal & Brosnan 2006, Rutte & Taborsky 2008), because inducing or manipulating natural helping acts that occur in the wild is difficult or impossible.

Common vampire bats (*Desmodus rotundus*) feed only on blood and die after 70 hours of fasting (McNab 1973), but unfed bats often receive food from roost-mates by regurgitation (Wilkinson 1984). Vampire bat food sharing is potentially a powerful model for understanding the cognitive enforcement of cooperation, because this behaviour is completely natural, energetically costly, occurs between kin and non-kin, and can be induced experimentally. Previous work found that free-ranging female vampire bats regurgitated blood mostly to their offspring (77 of 110 donations), but also fed adult females, preferentially close relatives and only frequent roost-mates (i.e. >60% co-roosting association; Wilkinson 1984). Hence, adult donations were predicted independently by relatedness and association. A captive experiment that induced food sharing among unrelated bats found that bats returned food donations to their past donors on 4 of 6 possible occasions— more than expected by chance (Wilkinson 1984). Although vampire bat food sharing has been a textbook example of reciprocity, this interpretation has been questioned due to several alternative explanations (e.g. Hammerstein 2003, Foster 2004, Stevens et al. 2005, Clutton-Brock 2009, Davies et al. 2012).

Wilkinson (1984, 1988) originally suggested that food donating vampire bats obtain both direct and indirect fitness benefits, with direct benefits outweighing kin-selected benefits. Under this scenario, cheating is prevented because bats donate preferentially to past donors and relatives. Hence, food-sharing decisions should integrate cues to kinship and future direct benefits (e.g. reciprocal donations or allogrooming, Wilkinson 1986).

Others have suggested that non-kin food sharing might simply result from manipulation (e.g. Clutton-Brock 2009). According to this "harassment hypothesis", non-kin food sharing benefits only recipients, not donors. Persistent begging by unfed bats might coerce conspecifics into food sharing. If so, donations should be solicited by recipients and directed primarily to dominant individuals.

Alternatively, donations to non-kin could simply be an incidental by-product of kin altruism. Hammerstein (2003) suggested that olfactory kin recognition cues could have been miscalibrated by the lack of kin present in the captive experiment (see also Stevens et al. 2005). This “miscalibrated kin recognition hypothesis” predicts that donors should donate almost exclusively to kin when in the more natural context of mixed relatedness.

Selection can favour indiscriminate altruism within social groups when the average within-group relatedness is high enough and the cost of helping is low enough. The “group-level altruism hypothesis” predicts that donors indiscriminately help groupmates (Foster 2004, Paolucci et al. 2006, Witkowski 2007). For example, Foster’s (2004) model of vampire bat food sharing “assumes that fed bats do not discriminate among unfed bats when giving blood” presumably because the costs of discriminating kin are too high.

Several simulations have been developed to explain food sharing (Foster 2004, Wilkinson 1988, Paolucci et al. 2006, Witkowski 2007), yet no one has gathered additional empirical evidence regarding how vampire bats decide to share food (but see DeNault & McFarlane 1995, Voigt et al. 2012). As a first step, we tested predictions of the above hypotheses by experimentally simulating unsuccessful foraging attempts in a captive colony of common vampire bats of mixed relatedness and equal familiarity. The original study (Wilkinson 1984) compared the explanatory roles of relatedness and association. Here, we directly compare relatedness and reciprocal help as predictors of food sharing, under conditions of equal association. We also evaluated alternative predictors of food sharing, including recipient age or size (as predicted by harassment) and food received from any groupmate (as predicted by generalised reciprocity: Pfeiffer et al. 2005, Rutte & Taborksy 2008).

Methods

Animals

All procedures were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-10-63). We did not test unhealthy bats, late pregnancy females, or mothers and their juveniles <4 months of age. We stopped testing males partway through the experiment since removing males coincided with increased aggression in the colony.

We fasted 11 males and 9 females out of 25 common vampire bats, descended from multiple matrilines. Bats were housed at the Organization for Bat Conservation (Bloomfield Hills, MI, USA) in a flight cage large enough to allow them to freely associate during the study and for >2 years prior. All bats were uniquely marked with passive integrated transponder (PIT) tags and coloured bands, except for three juveniles (4-8 months) born during the study that were reliably identified by PIT tags and distinctive face and body marks.

Fasting Procedure

To induce food sharing we removed and fasted a subject from the group for 24 h, then returned it to the cage with fed groupmates, and recorded subsequent social interactions for 2 h with a Sony Nightshot digital camcorder and infrared illumination. We measured the subject's mass immediately before reintroduction and after the 2 h observation period. We selected available bats randomly and without replacement to serve as subjects, and tested each subject 1-5 times. After the observation period, fasted bats were provided food.

Behavioural data

We refer to subjects that received food as ‘recipients’ and partners that provided food as ‘donors’. To quantify food sharing, we measured mouth-licking bouts via frame-by-frame analysis in iMOVIE 11. We defined mouth-licking bouts as periods where food could be passed that lasted at least 5 s and were separated by >5 s. We noted whether one bat clearly began licking a conspecific’s mouth and classified bouts accordingly as initiated by the recipient, donor, or ‘unknown’. We defined allogrooming as the licking of a conspecific at locations other than the mouth. To measure mean pairwise allogrooming rates, we randomly selected individuals for focal sample observations 1-4 times during non-trial days and counted the presence and direction of allogrooming with any conspecific every minute for 60 minutes.

We used mouth-licking time to estimate amount of food sharing because it strongly correlated with mass gain during the 2 h trial (r=0.90; 95% C.I.=0.73 – 0.96). We pooled time spent donating food from multiple days to obtain a single measure of food sharing for each directional dyad that had an opportunity to share food in each direction (n=312 dyads), except when we analyzed sequences of sharing events (see Appendix 2).

Pairwise relatedness

We extracted DNA from 2-3 mm biopsy punches using Qiagen DNeasy kits, then amplified and genotyped 13 microsatellite loci to estimate maximum likelihood coefficients of relatedness (r) for each dyad using ML-RELATE (Kalinowski et al. 2006, see Appendix 2). We jackknifed across loci to estimate standard errors (SE) for each r value (SE range=0-0.035; SE mean=0.005). Across all dyads, $r=0$ for 59%, $r<0.05$ for 69%, and $r>0.25$ for 20%. Patterns of observed and expected heterozygosity indicated no history of inbreeding (Appendix 2).

Statistical analysis

The variance in mouth-licking times increased with the mean, so we log-transformed mean food sharing time for each dyad (Appendix 2, Figure S1). We therefore defined "food donated" from bat A to B as ln ([total food shared A to B / chances for A to feed B]+1). We defined "food received" similarly, except with the roles of A and B reversed. We z-transformed all variables to standardize scales.

To analyse dyadic data we used a randomisation approach to general linear models, where we permuted food donated to sets of predictor variables creating a null distribution of comparison F values (Manly 2007). We first conducted univariate analyses to identify variables that predicted mean food donated across dyads, then performed a permuted multiple regression using the lmp function in the R package *lmPerm*. To choose the best model, we selected predictors and their interactions based on backward stepwise regression using Akaike and Bayesian Information Criteria in JMP 10. We interpreted interactions by examining correlations between two variables at several values of the other variables. To compare the relative importance of predictors, we averaged the sequential sum of squares over all orderings (Kruskal 1987) for up to three predictors using the R package *relaimpo* (Grömping 2006). We predicted amounts of food donated across directed dyads that could have shared food in both directions. We also predicted the presence or absence of food sharing across these dyads using logistic regression, and finally the amount of food donated only within dyads that did share food.

To determine if individual food donations were exchanged in a reciprocal manner over time (de Waal 1997), we examined the sequence of sharing events across trials to test for correlations between food given and received within dyads (using both amounts and proportions, see Appendix 2). To test the effect of general help received, we compared the mean amount of food donated by a bat to all fasted partners before and after it was fed by others to determine if it donated larger amounts after receiving food from others.

To test for symmetry and consistency of relationships, we used Mantel and randomisation tests to compare network similarity for (1) food sharing in subsequent fasting rounds, (2) food sharing six months apart, (3) allogrooming given and received, and (4) food sharing given and received, using only bats that both served as subjects and were available as donors in every round (Appendix 2).

Finally, to assess the harassment hypothesis, we examined whether recipients or donors were more likely to initiate mouth-licking. We also tested two potential measures of coercion ability, recipient age and size (forearm length), as potential predictors of food donated.

Results

Pattern of food sharing

We induced food sharing on 48 out of 52 fasting trials over 780 days, and recorded 950 food-sharing bouts. Food sharing occurred primarily between females and never between adult males (Figure S2, Appendix 2). Sixty-three of the 98 dyads that shared food had relatedness estimates <0.05. This percentage (64%) approaches that percentage expected (67%) if partners were chosen at random with respect to relatedness (i.e. 208 of 312 possible food-sharing dyads were related by <0.05).

In each trial, recipients were fed by an average of 3.9 donors (range=1-7). Median donation time per dyad in a trial was 191 s (N=204 donations, mean=339 s, range=5-3315 s). The total amount of food received from all donors during the 2 h period was typically about 5% of an adult recipient's mass, which restored ~20% of mass lost during 24 h of fasting (Appendix 2).

Predictors of food sharing across dyads

Univariate analyses showed that food donated was predicted by food received, allogrooming received, pairwise relatedness (Figure 1), and donor sex (included as a binary variable, Figure S4 in Appendix 2). All correlations were also significant before log transformations ($p<0.0002$ in all cases).

The best multivariate model (adjusted $R^2=0.372$, $F(5,306)=37.8$, $p<0.0002$) included food received ($\beta=0.319$, $p<0.0002$), donor sex ($\beta=0.267$, $p<0.0002$), allogrooming received ($\beta=0.186$, $p<0.0002$), and the interaction between relatedness and food received ($\beta=0.069$, $p=0.0276$), but not relatedness ($\beta=0.052$, $p=0.16$). An interaction plot showed that the relationship between food donated and received increased in slope with higher relatedness. Food received was 8.5 times more important than relatedness for predicting food donated (Figure 2).

Food received, donor sex, and allogrooming received, but not relatedness, also predicted the presence of food sharing (Appendix 2). Among the 98 food sharing dyads, donation size was predicted independently by food received and relatedness, with the latter relationship driven by mother-offspring pairs (Appendix 2).

Predictors of food sharing across trials

Sequential analysis across trial days indicated that the amount of food donated and previously received were correlated when comparing the proportion of a donor's contribution to the total food received by a partner (R^2=0.08, F(1,160)=13.9, p<0.0002), but not when comparing the absolute amount of food given and received (R^2=0.01, F(1,160)=2.4, p=0.1).

We found no evidence that being fed in general increased subsequent food sharing, as expected by generalised reciprocity (Appendix 2). Donation sizes could sometimes be compared both before and after the donor was fed within a round of trials. In these 28 cases, we failed to find a difference in presence of food sharing (paired t=0.98, df=27, p=0.34), total food donated (paired t=-1.3, df=27, p=0.20), or food donated per recipient (paired t=0.16, df=27, p=0.87). When the donor was fed on the previous day, we found no difference between the amount donated on that day compared to the donor's average on other days (n=9 donors and 9 trials, paired t=-0.013, df=8, p=0.99).

Consistency of social relationships

Dyadic relationships were consistent and symmetrical over time. Contrary to random association, food-sharing networks were significantly similar when comparing patterns 8 days apart (15 bats, amount shared: $p=0.0298$, presence of sharing: $p=0.0072$) or 6 months apart (67 dyads, amount shared: $p=0.0238$, presence of sharing: $p<0.0002$). Amounts given and received were correlated for both the food-sharing (15 bats, amount shared: $p=0.0004$) and allogrooming network (Figure 3).

Predictors of harassment

Donors initiated food sharing in 62% of non-maternal food sharing bouts. Mean duration did not differ between food sharing bouts initiated by donors versus recipients ($t=1.4$, $n=235$, $p=0.16$). We found no effect of recipient age ($R^2=0.006$, $p=0.2$) or forearm length ($R^2=0.004$, $p=0.5$) on amount of food donated.

Discussion

Predictors of food sharing

The relative importance of relatedness and reciprocal sharing in determining the food-sharing decisions of adult vampire bats was not directly comparable in previous work (Wilkinson 1984). Here, we found that, among captive vampire bats where co-roosting association is held constant, the predictive role of reciprocal help greatly exceeds that of relatedness. Food received from a partner was the strongest and most robust predictor of both the presence and amount of food donated to that partner. The donor's sex, amount of allogrooming received, and a positive interaction between food received and relatedness predicted food donated to a lesser extent.

Distinguishing the roles of direct and indirect fitness can be difficult because social behaviours, such as punishment or reciprocal help, can change the cost-benefit ratio in Hamilton's rule ($r>c/b$), leading to complex interactions between direct and indirect fitness benefits (Wilkinson 1988, Griffin & West 2003, West et al. 2007a, Ratnieks & Wenseleers 2008, Zöttl et al. 2013). For example, the predictive roles of reciprocal help and relatedness in food sharing could interact positively or negatively. Since vampire bats under the age of 2 years fail to feed on 30% of nights (Wilkinson 1984), the benefits of receiving food are likely age-dependent. We might therefore expect older bats to feed related young but not vice versa causing a negative relationship between the predictors, reciprocal help and relatedness. Instead, we found a positive interaction: highly related pairs engaged in reciprocal sharing that was more symmetrical than unrelated pairs. For example, the largest donations were four females feeding their juvenile (4 and 8 months) or subadult male offspring (19 and 31 months); in all cases, the offspring reciprocated with large donations to the unfed mothers.

Evidence for social bonds

Much emerging evidence links social bonds with direct fitness benefits in social mammals [e.g. Schülke et al. 2010 and references therein]. Wild female vampire bats have been observed still roosting together after 12 years (Wilkinson 1985), and several lines of evidence suggest that such long-term social relationships play a role in stabilizing food sharing. First, allogrooming appears to serve a social bonding function because it is uncorrelated with ectoparasite levels in the wild (Wilkinson 1986), and occurred commonly and symmetrically in the absence of visible ectoparasites (Figure 3). Second, dyads that share food performed more allogrooming on non-test days than non-sharing dyads (Figure 3). Third, food sharing and allogrooming were correlated across dyads (Figure 1), and food-sharing patterns were significantly consistent over days and months. Finally, male vampire bats rarely share food in the wild where their social relationships are transient (Wilkinson 1985), but will share food in captivity (DeNault & McFarlane 1995) where male associations are more stable. Taken together with the relatively weak correlation between the exact amounts of within-dyad food donated and received between trials, these findings are consistent with long-term social bonds involving mutual exchange of both food and grooming over long periods, rather than short-term turn-taking or calculated reciprocity (de Waal & Brosnan 2006).

Alternative explanations for non-kin food sharing

Contrary to predictions of the harassment hypothesis (Clutton-Brock 2009), donors were more likely than recipients to approach and initiate mouth-licking (Appendix 2), even when excluding mother-offspring donations. We also found no relationship between food sharing and recipient age or forearm size, both potential correlates of harassment ability. The harassment hypothesis therefore seems untenable as the sole explanation for non-kin food sharing.

Can vampire bat food sharing be explained by indirect fitness alone? Contrary to predictions of the miscalibrated kin recognition hypothesis (Hammerstein 2003), our results show that non-kin food sharing prevailed in a colony of mixed relatedness and equal familiarity. In this study, relatedness did not predict the presence or amount of food sharing across dyads that could have shared food. Although relatedness predicted donation size for food-sharing dyads, the effect was largely driven by extended maternal care (Appendix 2). One interpretation of these negative results is that kin discrimination is possible, but the indirect benefits of nepotism were overshadowed by the direct benefits of reciprocal food sharing. Alternatively, a group-level altruism hypothesis might predict that 'kin discrimination' is based on familiarity rather than phenotypic matching, leading to indiscriminate altruism within groups (Foster 2004).

The fission-fusion social dynamics of wild vampire bats lead to unstable roosting group membership, and male dispersal and occasional recruitment of unrelated females lead to low average relatedness in groups (r=0.02 to 0.11 based on genetic and pedigree analyses; Wilkinson 1985). Under such conditions, selection is not expected to favour kin recognition mechanisms based on familiarity alone. The multi-level selection model by Foster (2004) suggests that indiscriminate altruism within groups can be favoured at mean group relatedness levels as low as 0.05, but this model assumes that bats are neither cheating, reciprocating, nor nepotistic, as any of these strategies would make a system of indiscriminate altruism unstable. In contrast, we found that the network of food donations within the captive group was less random, more reciprocal, and more consistent over time, than expected by chance.

Free-ranging common vampire bats preferentially feed relatives within roosts despite frequent roost-switching and co-roosting with non-kin (Wilkinson 1984,

1985) indicating that vampire bats are capable of kin discrimination. While the mechanisms for kin or individual discrimination are still unclear, auditory and olfactory cues are likely. Female bats of all species recognize juveniles through isolation calls, and adult common vampire bats often produced similar individual-specific contact calls when isolated (Carter et al. 2012). Playback studies have demonstrated that such calls allow individual discrimination in the closest extant vampire bat species, *Diaemus youngi* (Carter et al. 2008). Food-sharing bouts were preceded by allogrooming and sniffing, which suggest a role for odour. Additional studies are needed to test recognition mechanisms in this species.

Evidence for reciprocity

The correlation we observed between food donated and received does not demonstrate that receiving food determines subsequent food donated within a dyad. For this reason, we avoided the term "reciprocity" to prevent confusion because the term has broad, narrow, and sometimes contrasting definitions in the literature (see Chapter 1). Reciprocity could involve partner control through direct reward or punishment within dyads, or partner choice and switching based on the perceived relative value of different partners as co-operators (e.g. Noë & Hammerstein 2003, Bshary & Grutter 2005, 2006; Rutte & Taborsky 2008; Fruteau et al. 2009). Experiments are needed to test if and how donors respond to cheating.

We found that on average fasted bats were fed by three donors, so the costs of food sharing were often divided among partners. As expected, potential donors sometimes rejected begging recipients, but unexpectedly, some fasted subjects also appeared to reject food offers from some potential donors. This surprising observation may indicate that bats favour some food-sharing partners over others, with implications for modelling vampire bat cooperation as a biological market (Noë & Hammerstein 1994, Fruteau et al. 2009) rather than as an iterated dyadic interaction.

Acknowledgements

We thank the Organization for Bat Conservation, Rob Mies, Jesse Fabian, Mary Smith, and Matthew Mulkeen for their generous support. Work was funded by grants-in-aid of research from the Cosmos Club Foundation, American Society of Mammalogists, Explorer's Club Washington Group, and Sigma Xi. GGC is supported by a Ford Foundation Predoctoral Fellowship, administered by the National Academy of Sciences.

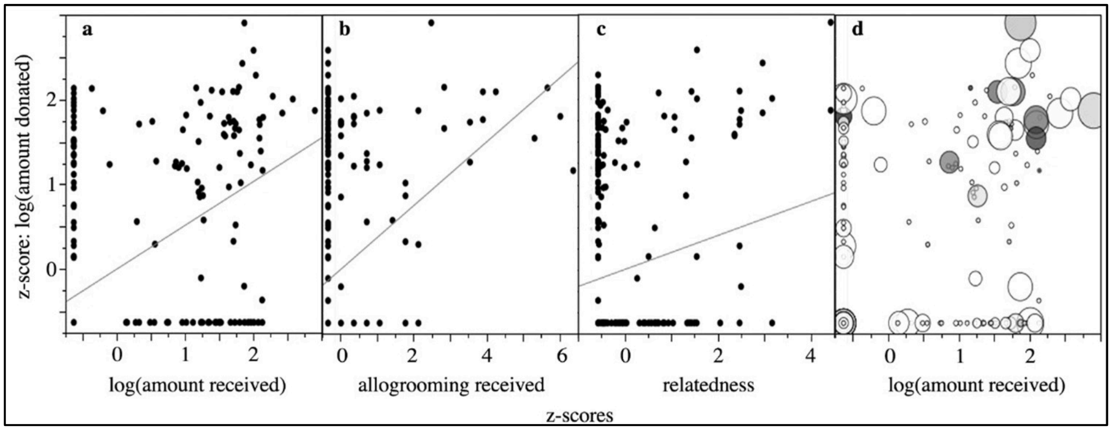


Figure 1. Relationships between food donated and predictor variables. Z-score for log food donated was predicted by z-scores of (a) log food received (R^2=0.27, p<0.0002), (b) allogrooming received (R^2=0.14, p<0.0002), and (c) relatedness (R^2=0.04, p<0.0012). A bubble plot (d) shows multivariate relationships by scaling bubble size to relatedness and bubble darkness to allogrooming received.

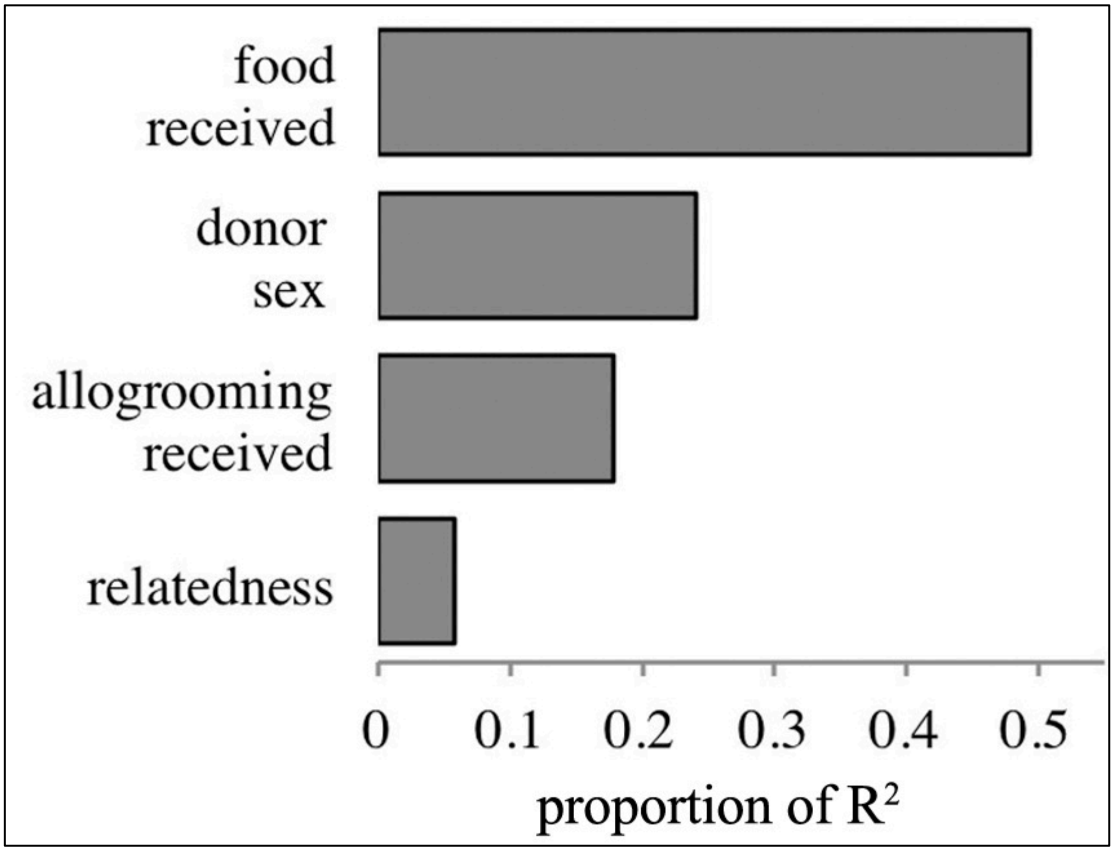


Figure 2. Relative importance on food donated of several predictors. Proportion of R^2 is shown for four predictor variables. An interaction effect (see text) is not shown. The full model explained 38% of the variation in food donated.

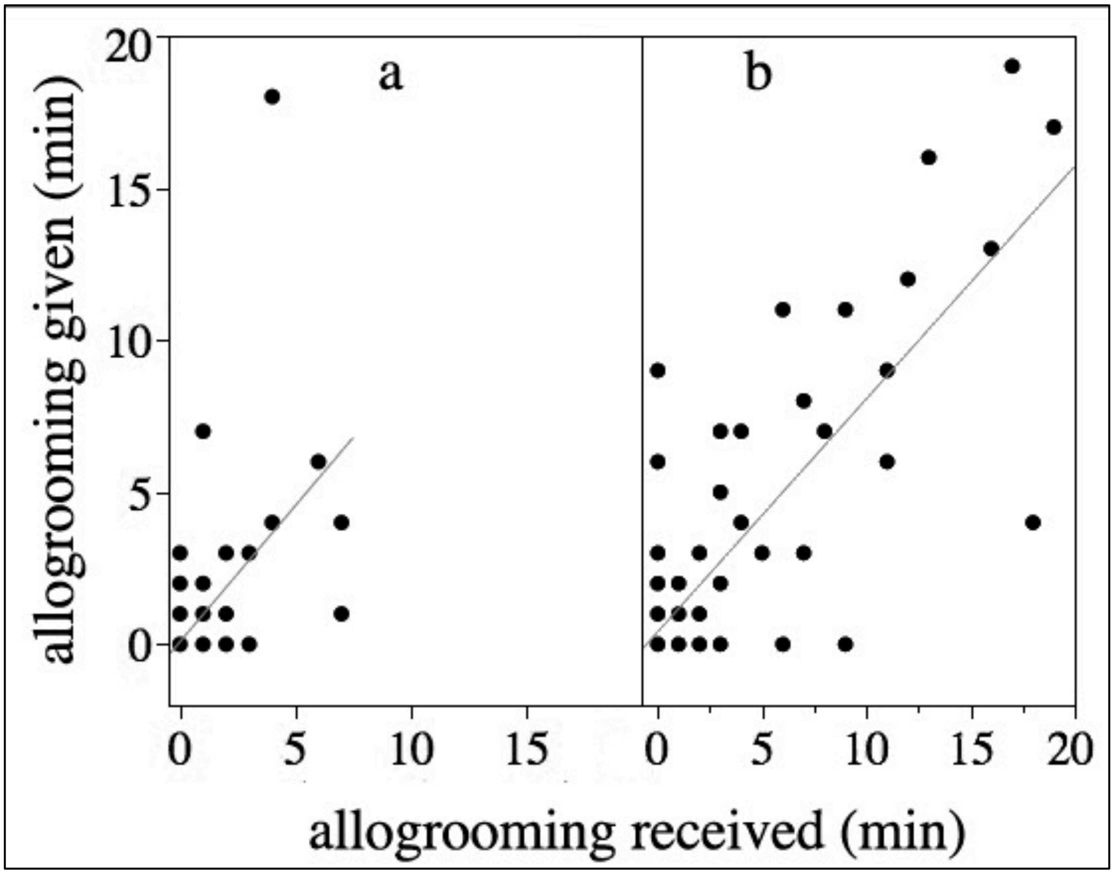


Figure 3. Allogrooming given correlates with allogrooming received.

Allogrooming giving is plotted against allogrooming received for dyads that did not share food (a, n=214, r=0.62, p<0.0002) and dyads that did share food (b, n=98, r=0.81, p<0.0002). On non-trial days, dyads that shared food both gave and received more allogrooming than non-sharing dyads (F(1,310)=32.9 and 41.0, p<0.0002 for both).

Chapter 3: Intranasal oxytocin increases social grooming and food sharing in the common vampire bat *Desmodus rotundus*

Abstract

Intranasal oxytocin (OT) delivery has been used to non-invasively manipulate mammalian cooperative behavior. Such manipulations can potentially provide insight into both shared and species-specific mechanisms underlying cooperative behaviors. Vampire bats are remarkable among mammals for their high rates of allogrooming and the presence of regurgitated food sharing among adult females. We administered intranasal OT to highly familiar captive vampire bats to test for an effect on allogrooming and food sharing between related and unrelated adults. We found that intranasal OT did not have a detectable effect on the occurrence of food sharing, but it did increase the size of regurgitated food donations after controlling for dyad and amount of allogrooming. Intranasal OT in females increased the amount of allogrooming per partner and across all partners per trial, but not the number of partners. We also found that the peak effect of OT treatments occurred 30-50 minutes after administration, which is consistent with past data on the latency for intranasal OT to affect relevant brain areas in rats and mice. We suggest that measuring prior social relationships can help interpret the results of hormonal manipulations of cooperative behavior, and that intranasal OT is a potential tool for influencing dyadic cooperative investments, but it may be difficult to alter partner choice in vampire bats using intranasal OT alone.

Introduction

Social mammals make frequent decisions regarding when and how much to invest in cooperative behaviors. These decisions depend on an interacting suite of internal and external factors and often culminate in complex long-term social relationships. To determine the consequences of these decisions, it would be desirable to manipulate the size of cooperative investments from one animal to another. One promising tool for experimentally manipulating mammalian social behavior is the neuropeptide oxytocin (OT, reviewed by Crockford et al. 2014 and refs therein). Peripheral OT administration can experimentally increase the cooperative investments of targeted individuals without highly invasive procedures (e.g. Madden et al. 2011), and it affects a wide variety of species-specific cooperative behaviors (e.g. humans: Bartz et al. 2011, Veening & Olivier 2013; macaques: Simpson et al. 2014; marmosets: Smith et al. 2010; meerkats: Madden et al. 2011; naked mole-rats: Mooney et al. 2014; rats: Calcagnoli et al. 2015; dogs: Romero et al. 2014). Oxytocin manipulation thus provides a method for identifying mammalian social behaviors that share a common mechanism.

We tested for effects of intranasal OT on food sharing and allogrooming in the highly social common vampire bat (*Desmodus rotundus*). These bats feed only on a single meal of blood per night, can starve in <72 hours, and often fail to obtain meals (with 18% of 598 bats failing to feed on a given night), but young bats and adult females that fail to feed often solicit regurgitations of blood from familiar conspecifics (Wilkinson 1984). Female common vampire bats form stable and symmetrical networks of regurgitated food sharing and allogrooming, both in the wild (Wilkinson 1984, 1985) and captivity (Carter & Wilkinson 2013a, 2013b). Some free-ranging females maintain these associations for more than a decade even under conditions of frequent roost switching (Tschapka & Wilkinson 1999). Allogrooming and food sharing events are correlated across dyads and over time, with allogrooming often occurring immediately before sharing, suggesting that allogrooming may serve in facilitating social recognition, assessing the ability to give (Wilkinson 1986), signaling a desire to receive (i.e. begging), or signaling intention to share (Carter & Wilkinson 2013a). Using familiar captive vampires bats, we asked the following questions. Does intranasal OT increase allogrooming and food sharing? And if so, does OT increase cooperative investments with established sharing and grooming partners, broaden investments to more partners, or promote increased investments to fewer partners?

Methods

Food sharing

We tested if oxytocin (OT) affects food sharing in five (four female, one male) common vampire bats (*Desmodus rotundus*) on 39 trial days from Sept 17, 2013 to Dec 16, 2013. We prepared OT treatments by mixing OT (Bachem, USA) into saline solution at a concentration of 0.45 μg/μl and treated bats by slowly pipetting 5 μl of solution at a time into each nostril of a bat with a micropipettor allowing 5-15 s between each intranasal dose. If bats sneezed during the treatment, we administered another 5 μl of solution.

For each trial day, we first removed and fasted a subject bat while the other four bats were fed blood *ad libitum* in a 1.7 x 2.1 x 2.3 m cage for 24 h. We then randomly treated two fed bats with OT and two fed bats with saline, returned the fasted bat to the four treated fed bats in their home cage, and observed interactions for 2 h with a Nightshot camera (Sony, USA) and infrared spotlight (IRlamp6, Wildlife Engineering, USA). For each min, we scored the presence (>5 s) of mouth-licking and allogrooming (defined as one bat licking, chewing, sniffing, or nuzzling another bat's body). We measured the subject's mass to the nearest 0.01g (model L125 digital scale, Escali, Burnsville, MN, USA) immediately before and after observation. We defined "donation size" as the total mouth-licking time between two bats in a trial that led to subsequent mass gain in the fasted subject.

Subjects were not fasted again until all other bats served as subjects, but otherwise bats chosen for fasting or OT treatment were selected at random. In our last four trials one female was removed from the experiment, and we stopped our experiment at 39 trials due to suspected illness in the colony, which led to bats serving as fasted subjects an unequal number of times (31, 31, 23, 35, 32), and potential donors being treated with saline/OT an unequal number of times (14/17, 15/16, 16/17, 16/14, and 14/13).

We estimated kinship among individuals using a maternal pedigree, 30 polymorphic microsatellite markers, and the program ML-RELATE (Kalinowski et al., 2007). We log-transformed both donation size and allogrooming duration so that neither deviated significantly from normality (Shapiro Wilk's W=0.98 and 0.95, p>0.05). We used Chi-square tests to test the effect of subject, donor, and treatment on the presence or absence of a donation across all opportunities. For all observed donations, we tested which factors (allogrooming, treatment, dyad, kinship, and the interaction between kinship and treatment) predicted donation size using minimum AIC and backward stepwise regression for model selection in JMP 11 (SAS 2013). Our best model for donation size included treatment and allogrooming as fixed factors, and dyad as a random factor.

Allogrooming

To determine if intranasal OT influences allogrooming, we conducted a double-blind study where 13 adult females were treated with intranasal OT or saline at the same hour on two consecutive days. Doses of OT (1 μg/μl) and saline controls were randomly scheduled and labeled with numbers to conceal their identity during treatment. On the first day, we treated a bat as described above with saline or OT between 1600—2100h, placed it in a 1.5 x 2 x 3 m home cage with 14 other adult females, 22 adult males, and one juvenile male. We then recorded interactions with a Sony Nightshot camera and infrared spotlight for 1 hour. For each minute we then scored the presence (>5 s) or absence of allogrooming, the identity of the allogrooming partner, whether allogrooming was given or received, self-grooming, and physical contact without allogrooming. At the same time on the next day, the same bat received the opposite treatment.

We focused on female allogrooming, because most allogrooming in the wild occurs among adult females and juveniles of both sexes (Wilkinson 1986) and many of the males had been castrated. In pilot trials, we also failed to detect an effect of oxytocin on young males isolated with their mothers (see Appendix 3).

We used Wilcoxon Signed Rank tests (and report the statistic, S) to compare the effect of treatment on each response paired within bat. To test if oxytocin influenced the extent to which bats preferentially groomed relatives, we first multiplied duration of allogrooming with each partner by that partner's kinship, and then averaged across partners in that trial to calculate a nepotism index for each trial. The greater the nepotism index, the more allogrooming was targeted towards kin. For all cases where allogrooming partners in both trials were identified, we compared the nepotism index by treatment. All procedures involving animals adhered to the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-13-30).

Results

Food sharing

Food sharing was evident in fasting trials because total mouth-licking time predicted a recipient's subsequent weight gain (R^2=0.63, $p<0.001$). However, food sharing occurred in only 16 of 39 fasting trials (38 donations out of 152 possible dyad-trial cases). We detected no effect of treatment on the presence of food donations, which occurred 19 times in each treatment condition. The occurrence of food sharing instead varied largely by subject-donor dyad (c^2=59.29, $p<0.0001$).

For the 38 confirmed donations, we found that donation size increased with both OT treatment (R^2=0.61, $F_{1,34.1}$ = 11.43, p=0.0018; least squares means +/- standard error: saline treatment=1.20 ± 0.26, OT treatment=2.13 ± 0.26) and allogrooming (log-transformed; $F_{1,23.66}$=67.51, p<0.001). Higher kinship did not predict occurrence of food sharing; in fact mean kinship was lower for sharing events than non-sharing events across both treatments. Kinship also did not increase donation size (log-transformed, $F_{1,14.61}$=0.0053, p=0.94), and when we included kinship and the kinship by treatment interaction in our model, neither factor was significant.

Allogrooming

OT treatment of females did not change the number of groomers (S=2.6, p=0.22), the number of grooming recipients (S=0.5, p=0.48), or the amount of physical contact (S=15.5, p=0.30, Figure 4A), but it did increase the number of minutes a treated animal engaged in allogrooming overall (S=41, n=13, p=0.002, Figure 4B) and per partner (S=5.7, p=0.034). By analyzing the number of grooming bats and the effect size at each minute across the trial, we found that the peak effect of OT treatments occurred 30-50 minutes after administration (Figure 5).

For the 8 subjects with known grooming partners in both treatments, we failed to detect an effect of treatment on the nepotism index (Wilcoxon Signed Rank S=0.5, p=0.50). Most grooming occurred between unrelated bats (63% of grooming dyads in trials had estimated kinship values of <0.05, mean kinship=0.09), and there was only one dependent pup present at the time. There was a trend towards females grooming this pup more when they were dosed with OT (paired t=2.59, n=5, p=0.061).

Discussion

Oxytocin (OT) increased cooperative investments within existing social bonds, but we did not find strong evidence that it either extended investments to more partners, or increased investments in fewer partners. The physiological mechanism by which inhaled OT affects behavior remains unclear, but studies with rats and mice revealed that intranasal OT administration first increased plasma levels, and within the next 30 minutes led to increased OT in behaviorally relevant brain areas (Neumann et al. 2013). Our data are consistent with these observations in that allogrooming was elevated 30-50 min after intranasal OT exposure (Figure 5).

Over a period of three months, we tracked food-sharing donations among five vampire bats (20 dyads), and found that OT treatment increased donation sizes within dyads, but did not affect the probability of a given dyad to share food. Our second study showed that OT increased female allogrooming within dyads, but did not alter the number of grooming partners. These two findings indicate that OT inhalation has partner-specific effects on social investment.

Increasing evidence suggests that the link between cooperative behavior and OT depends on the subject's prior relationship with the partner, exaggerating pre-existing social predispositions to particular individuals or categories of individuals (Crockford et al. 2014 and refs therein). The relationship between prior social bonds and OT response is further complicated by the fact that peripheral OT induces cooperative behavior, but is also released by it (Crockford et al. 2014). OT-induced behaviors or cognitive states can lead to further OT release resulting in a positive feedback loop that may be important in the development of social bonds. Interpreting the relationship between oxytocin and behavior can therefore be limited by knowledge of an individual's prior social relationships. For example, elevated urinary OT in wild chimpanzees is caused by both the giving and receiving of allogrooming and food sharing, but the effect of food sharing on subsequent urinary OT is stronger and more consistent across partners compared to the effect of allogrooming, where the release of OT depends on the strength of the existing social bond (Crockford et al. 2013, Wittig et al. 2014). Given this complex interaction between OT and social experience, much can be learned by further studies pairing OT manipulation with long-term observations of marked individuals with known social histories, social bonds, and kinship relationships.

Acknowledgements

We thank K. Thompson for suggestions that improved the manuscript, L. Leffer for help with data collection and the Organization for Bat Conservation for animal care. This work was supported by a National Science Foundation Doctoral Dissertation Improvement grant (IOS-1311336) to GSW and GGC and a Ford Foundation Fellowship administered by the National Research Council of the National Academies to GGC.

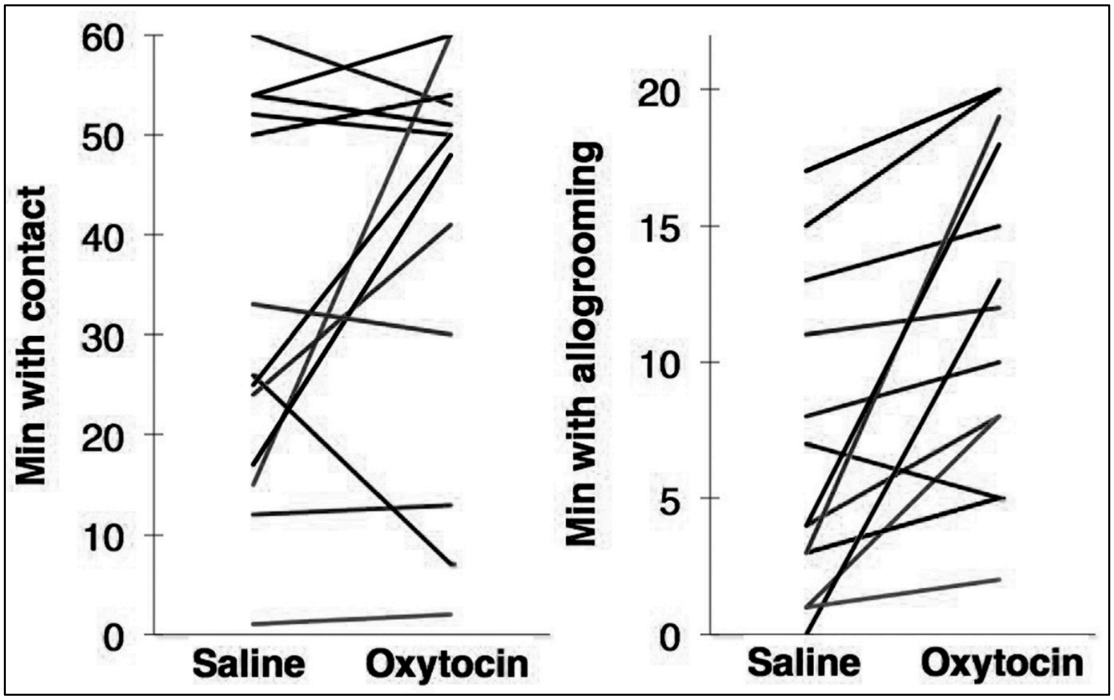


Figure 4. Oxytocin affects allogrooming but not physical contact. Lines show changes in time spent in physical contact without allogrooming (A) or allogrooming (B) in female vampire bats when dosed with either oxytocin and saline.

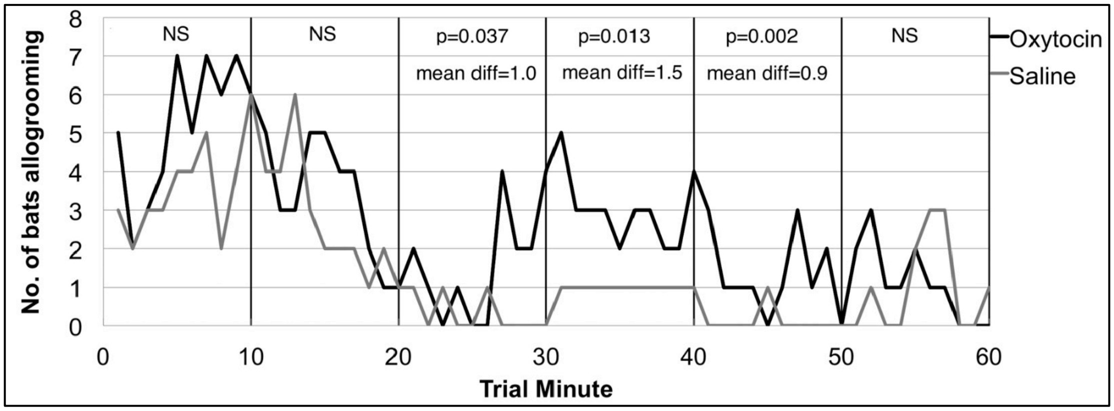


Figure 5. Latency of effect of intranasal oxytocin on allogrooming. Lines show number of bats that groomed others during that minute of the trial when dosed with oxytocin (blue) or saline (red). Significance (two-tailed p-value or NS) and difference between bat-centered treatment means is shown for each 10-min segment. Time zero marks the treated bat's release into the cage.

Chapter 4: Vampire bats do not play strict ‘tit for tat’ when sharing food

Abstract

Reciprocity is often interpreted as a ‘tit-for-tat’ rule where giving help is strictly contingent on receiving help. Food sharing among kin and non-kin vampire bats (*Desmodus rotundus*) shows a highly reciprocal pattern, but are these food-sharing investments strictly contingent on recent returns? We tested the contingency of food-sharing bonds in 7 unique vampire bat dyads that had histories of sharing (14 female ‘subjects’ and ‘primary donors’ including four mothers and their four adult daughters). In each of 84 fasting trials, we fasted the subject for 24 h to induce and measure food donations from all others, while another bat was excluded from the donor pool. Each subject served in a series of fasting trials where we first excluded a low-ranking donor, then excluded the primary donor three times; and finally removed a low-ranking donor again. During this experiment, females that fed more bats before the experiment, also received more food per experimental trial. When we first removed primary donors, subjects did not compensate with donations from other bats, so they received less food. Despite preventing dyadic food sharing on 3 occasions over 3 weeks, we detected no subsequent change in food sharing. Comparisons of kin with non-kin were hampered by sample size, but maternal kin were clearly not enforcing cooperation using strict contingency alone. We discuss how kinship and stable social bonds are likely to influence enforcement via contingency. It is

increasingly clear that vampire bat food-sharing deviates from literal interpretations of the tit-for-tat model.

Introduction

Cooperative organisms are expected to target their cooperative investments to partners that provide the best inclusive fitness returns. Organisms can ensure indirect fitness benefits by discriminating among partners based on kinship (Hamilton 1964, Griffin & West 2003), or they can enforce reciprocal direct fitness benefits by discriminating among partners based on cooperative returns (Trivers 1971, Rutte & Taborsky 2008, Krams et al. 2008, 2013, Kiers et al. 2011, Dolivo & Taborsky 2015, reviewed by Carter 2014). Importantly, although kin discrimination and enforcement of fitness benefits are often considered as alternative explanations for cooperation, they may co-occur and interact (evidence: Koenig 1994, West et al. 2007a, Ratnieks & Wenseleers 2008, Zöttl et al. 2013, theory: Frank 1995, Van Cleve & Akçay 2014).

Using observations of cooperation among common vampire bats (*Desmodus rotundus*), Wilkinson (1984, 1988) argued that reciprocity could stabilize cooperation among relatives. Female vampire bats regurgitate portions of ingested blood meals to both related and unrelated adults. Although 95% of these donations observed in the wild occurred between relatives, food sharing was even better predicted by prior interactions, and reciprocal sharing occurred readily between non-kin (Wilkinson 1984). To assess the relative importance of kinship and social experience on vampire bat food sharing, Carter & Wilkinson (2013a) induced over 200 regurgitations under controlled conditions of constant association and mixed relatedness. Results supported the hypothesis that non-kin food sharing provides direct fitness benefits and that sharing decisions are not easily explained as a kin selection byproduct (Carter & Wilkinson 2013a,b). But two key issues remain unresolved.

First, demonstrating reciprocity requires testing contingency, which has not been shown experimentally in vampire bats. While some authors use the term "reciprocity" to describe correlations between help given and received (e.g. de Waal & Luttrell 1988, Hemelrijk 1990, de Waal & Brosnan 2006), such network correlations can result from helping decisions based on any symmetrical social factor, including kinship, proximity, or group membership (Figure 6). For clarity, we use the term "symmetry" to describe positive *correlations* between help given and received across pairs, and reserve the term "reciprocity" for adaptive cooperative investments that are in some way *contingent* on cooperative returns. Dyadic correlations of help over time may be suggestive of contingency (e.g. de Waal 2000, Johnstone et al. 2014), but a convincing demonstration typically requires measuring the extent to which individuals shift their investments either away, or towards, partners whose ability to provide cooperative returns has been experimentally diminished (e.g. Kiers et al. 2011), or enhanced (e.g. Fruteau et al. 2009).

Testing contingency in vampire bats has proven difficult because fasting events must be separated in time both to protect the health of the animals and because overall sharing decreases over time with repeated fasting. Authors often assume that the timescale of contingency should be short and strict, following a literal translation of "tit for tat" (Axelrod & Hamilton 1981, reviewed by Carter 2014), but evidence for strict within-dyad symmetry over time (symmetrical matching and turn-taking) in vampire bat food-sharing is weak (Carter & Wilkinson 2013a). Rather, dyadic food sharing becomes balanced over time.

Vampire bat food sharing is also highly sensitive to context. We failed to induce food sharing across about 40 fasting trials using isolated vampire bat pairs or triads in small cages. Bats reliably share food when tested in a familiar group setting, but this involves statistically or experimentally controlling for the presence of multiple possible partners. Testing contingency in a short timeframe also requires reducing help from partners that are reliable and consistent donors. Such donors are often matrilineal kin, which brings us to the second issue: the expected degree of contingency between genetic relatives is unclear.

Depending on the relative importance of direct (reciprocal) and indirect (kin-selected) fitness benefits in food sharing, the degree of reciprocity can interact with kinship in either a positive or negative manner. Wilkinson's (1988) model of vampire bat food sharing suggested that the reciprocal (direct fitness) benefit of sharing exceeds any kin-selected (indirect fitness) benefit, at all levels of kinship. Under this scenario, the main return on investment in food sharing is an increase in personal survival and reproduction (direct fitness) due to reciprocal help rather than an increased survival of kin (indirect fitness). Accordingly, it is possible that close kin pairs, such as mothers and their adult daughters, might show the strongest contingency in sharing because they make the largest investments in each other. Such individuals may find the experience of non-reciprocation from these partners to be the most unexpected, salient, and costly. This notion is consistent with the observation that more related bats have more balanced sharing (Carter & Wilkinson 2013).

Alternatively, if food sharing among kin is driven by indirect fitness benefits, then it may be largely altruistic, so close kin pairs might show less or no contingency. This kind of negative interaction between kinship and the enforcement has been found in cooperatively breeding cichlids, where subordinate helpers exchange alloparental care for the ability to stay in the group, but related subordinates are tolerated more and hence provide less alloparental care in return (Zöttl et al. 2013). Similarly, non-reciprocation may be tolerated more by related vampire bats.

To test these alternative predictions, we assessed food-sharing contingency in both related and unrelated pairs of female vampire bats. We attempted to redirect the food-sharing investments of bats away from a reliable and consistent donor towards other partners. We first measured the stability and symmetry of the food-sharing network using data on allogrooming, food sharing, and kinship among a group of 24-32 captive vampire bats over a 4-year period. We then selected 14 directional dyads by pairing each subject with a unique 'primary donor' that consistently shared food. These dyads included four pairs of mothers and their adult daughters with strong sharing histories, and three dyads of unclear or zero kinship. We measured within-dyad food given and received across two fasting rounds when they could feed each other. Then, we fasted both bats in each dyad simultaneously on 3 treatment rounds over 3 weeks, such that neither bat could feed their primary donor but each could be fed by others. After this treatment, we again allowed and measured food given and received within each dyad.

We had three predictions. First, if food sharing is based on stable social bonds, then removing the primary donor, rather than a non-bonded partner, should lead to a decrease in total food received in that trial. Second, we predicted that females with larger sharing networks (measured before the experiment) would be fed more during the experiment. Third, if food sharing was highly contingent on past sharing, then we expected both the amount and proportion of reciprocal food sharing with the targeted primary donor to decrease.

Methods

General methods

All procedures were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-10-63). Animal care and methods for inducing food regurgitations are described elsewhere (Carter & Wilkinson 2013a). Briefly, we housed vampire bats in a captive colony of 25-45 animals from multiple matrilines. To induce food sharing, we removed and fasted 1-2 subjects, returned the first bat to the group cage for a 1 h focal sampling observation period, and then the second bat for another 1 h observation. All bats were then fed. By measuring the mass of bats immediately before and after observation, we found that time spent mouth-licking was a good predictor of mass gained by the end of the observation period ($r=0.9$). Seconds of mouth-licking is therefore a measure of food-sharing that is unaltered by urinating or defecating. We defined ‘food given’ for each directional pair as the natural log of ($X+1$) where X is the total seconds of food-sharing from A to B divided by number of 1 h trial chances for A to feed B. We defined ‘food received’ in the same way, with roles of A and B reversed.

Analysis of the baseline long-term food-sharing network

To test network correlations via permutation, we used Hemelrijk's (1990) Kr tests and partial Rr tests in SOCPROG 2.5 (Whitehead 2009). These tests indicate if food given (A to B) is correlated with food received (B to A) relative to the food received from all other bats that could have been donors (i.e. 'relative reciprocity' Hemelrijk 1990). Food sharing and allogrooming network tests used only pairs that had chances to give and receive. We calculated kinship using known birth dates, maternal pedigree, and maximum-likelihood estimates of relatedness calculated in the program ML-RELATE (Kalinowski et al., 2007) from genotypes of 30 polymorphic microsatellite markers (Appendix 4, Table S2, S3). We amplified PCR products from DNA extracted from 2-3 mm wing punches using Qiagen DNeasy kits.

Contingency experiment

Our goal in this experiment was to first weaken food-sharing relationships between specific pairs by repeatedly inhibiting dyadic food sharing, and then test if we could detect a change in the food given when dyadic food sharing was again possible. We selected 14 directional dyads by pairing each subject with a unique primary donor where donations had previously occurred most reliably and often in both directions, but not all bats could be paired with their highest-ranking donor (Table S1).

We paired as many females as possible with their most preferred sharing partners, typically their mother or adult daughter (8 maternal kin dyads, Table S1). We did this for two reasons. First, we required strong dyads with consistent sharing histories to maximize the probability that the targeted donor would feed the subject during the prior baseline period. Any experimental decrease in donation rate is easier to detect in dyads with larger, more frequent donations. Second, although contingency is most expected between non-kin, it would be most interesting and surprising to see contingency as an enforcement mechanism between relatives. Thus, this design allowed us to determine if contingent reciprocity operates between close kin.

Across 84 fasting trials, we put each subject through 6 rounds of fasting: two pre-treatment rounds, three treatment rounds, and one post-treatment round. We fasted two bats a day, so each round required 7 days. During each round, we fasted two females simultaneously on each trial day such that one bat could not feed the other because it was absent or unfed, but so that each bat could be fed by 13 other females or 11-15 males (Figure 7). All other males were placed on the other side of a mesh curtain. During the three treatment rounds, we simultaneously fasted our selected pairs. During pre- and post-treatment rounds, we simultaneously fasted pairs with little or no history of sharing (Figure 7).

We were first interested in whether each subject's primary donor would be replaced by other donors when the primary donor was missing or unfed. When a subject's primary donor was unavailable, would that subject receive the same total amount of food? To answer this question, we tested whether the total food received (paired by subject) differed between the pre-treatment and treatment rounds. To ensure that any decline we observed actually occurred when the subject was first removed, we calculated the change in total food received from the previous round (current round minus previous round) for each bat. To examine which rounds showed significant declines in total food received, we calculated the mean and 95%

confidence interval of the change, and tested whether the decline in total food received by subjects during round three (when the primary donor was first removed) was on average a greater decline than the mean for the other rounds.

Our main interest was in the contingency, reflected by the change from the pre-treatment to post-treatment for each subject. Using both absolute values and arcsin-transformed proportions of total food received, we compared the mean amounts of food received from primary donors during pre- and post-treatment rounds. We used paired t-tests because the distributions of changes in total food received (food received in current – previous round) were highly normal overall (test of deviation from normality: Shapiro-Wilk W= 0.99, p=0.9) and within each round (W range=0.94-0.98). To examine the effect of a subject's sharing network size on subsequent sharing success, we used linear regression to test (1) if females that fed more partners from 2010-2014 had more donors in the contingency experiment, and (2) if the number of donors a subject had on average during the experiment explained between-subject variation in total food received.

For all parametric tests, we tested for deviations from normality using a goodness of fit test. We conducted all t-tests assuming unequal variances in JMP 11 (SAS 2013). When normality assumptions were violated, we calculated permutation p-values using the lmPerm package in R. To help interpret null results, we present 95% confidence intervals rather than post hoc power analyses, which are easily misinterpreted (Heonig & Heisey 2001, Levine & Ensom 2001).

Results

Food-sharing network symmetry and stability

The vampire bat food-sharing network from 2013-2014 was both symmetrical and consistent with data from previous years (2010-2012 network data from Carter & Wilkinson 2013; Hemelrijk Kr-test, p<0.0002, n=30 in both cases). Similar to past results (Carter & Wilkinson 2013), subsequent patterns of food-sharing were not well predicted by kinship (p=0.3), but were predicted by allogrooming (p<0.0002). Female allogrooming networks in 2014 were not correlated with kinship (p=0.5), but were consistent with measures from 2012 (p<0.0002, data from Carter & Wilkinson 2013). Pairs that allogroomed when sampled in 2012 were more likely to groom when sampled in 2014 (Fisher's exact test: p<0.0001). Using all data from 2010-2014, food-sharing symmetry remained significant when controlling for either kinship (Hemelrijk partial Rr-test, p<0.0002) or grooming received (p=0.0066, Appendix 4).

Contingency experiment

Removing a subject's 'primary donor' led to a decrease in the total food it received. Subjects received a mean of 227 s less food sharing when their primary donor, rather than another bat, was removed from the donor pool (paired t=-3.23, df=13, p=0.0066), and this decline in food received occurred during the round when the primary donor was first removed (Figure 8). The mean decline in food received during this round (mean=224 s, 95% CI=54--394 s) was greater than the mean change during all other rounds (t=3.14, df=29.3, p=0.0038; Figure 8).

Treatment did not noticeably affect the number of donors. We did not detect a significant change in the number of donors when the primary donor was first removed (mean=-0.36, 95% CI=-0.84 to 0.13 bats), nor did the change differ from the other rounds (t=0.54, df=35.1, p=0.6). We also did not detect fewer donors in trials where a subject's mother or daughter was present (t=0.03, df=40, p=0.97). The mean number of donors across all trials was 2.6 bats (95% CI=2.3--2.9).

Females with larger sharing networks were fed more during the experiment. Females that fed more bats in our 2010-2014 dataset, collected before the contingency experiment, subsequently had more donors during the experiment (R^2=0.30, F(1,12)=5.04, n=14, permutation p=0.044). The number of donors a subject had averaged across all experiment rounds explained 53% of the between-subject variation in food received (also averaged across all rounds; F(1,12)=13.3, p=0.0034).

Food-sharing bonds were robust to three fasting rounds without dyadic sharing. When comparing the pre-treatment to post-treatment period, we detected no within-dyad change in absolute food received from the donor (mean=-20.68 s, 95% CI=-177 to +136 s, t=-0.29, df=10, p=0.77; Figure 9) or in the donor's proportion of the total food received (mean=+18%, 95% CI= -34% to +70%, paired t-test with arcsin-transformed proportions: t=0.78, df=10, p=0.45; Figure 10). Food received from the primary donor post-treatment was greater than during the treatment, i.e. zero (permutation Z test, Z=2.52, one-sided p= 0.006), and it showed a rebound to near its original level (Figure 10).

In only three of seven possible cases did the maternal kin donors feed their partner a lower proportion of the total received after the treatment trials (E, J, K;

Figure 11). We lacked the ability to detect a treatment effect in three of the other subjects (bats B, C, O; Table 1), because they were not fed by their ‘primary donors’ during the two pre-treatment rounds. Since these dyadic sharing values could not be decreased further, we excluded these bats from the contingency analysis. But including these 3 bats did not change our main results. After the treatment trials, two of the three remaining non-kin subjects were fed by the targeted donor less (M, N) and one was fed more (P), with the sharing amounts measured either absolutely or as percentages of the total (Figure 11).

Because we removed half the non-kin subjects from the analysis, the rebound in sharing was driven primarily by the four mother-daughter pairs (Figure 10). Compared to the three non-kin donors that did feed each other, the four mothers and four adult daughters gave on average 176 s more food (95% CI=39--313 s, t=2.9, df=8.75, p=0.0175) and provided 44% more of the total food received by subjects (95% CI= +22--67%, t=4.6, df=7.17, p=0.0023; Figure 10). However, we failed to detect a difference between maternal kin and non-kin with regards to the change in sharing between pre-and post-treatment (absolute value: t=0.62, df=5.1, p=0.6; proportion of total: t=0.93, df=8, p=0.4).

Discussion

We found no evidence for short-term contingency. After 3 weeks of sharing with other partners, food sharing within the pairs we targeted rebounded to near their original levels. When ‘primary donors’ were first removed, subjects could not replace their food sharing contribution using other partners. This confirms past evidence that food-sharing is based on dyadic social bonds rather than on group or network-based familiarity (Carter & Wikinson 2013a,b). Female bats have networks of multiple donors that vary in size (this study: mean= 2.5, range 0—6 bats), and the size of a female bat's donor network was correlated with the number of bats it fed in the past. The number of donors a bat had in the contingency experiment explained about half the variation in total food received among bats (Appendix 3, Figure S7). Yet females cannot easily or quickly replace the help from their primary donors, especially maternal kin, with other partners. Both quantity and quality of social bonds matters.

The results of our study must be interpreted with several limitations in mind. First, we lacked the power to reliably compare any difference in contingency between kin and non-kin, since 3 of 6 non-kin donors did not initially donate during the pre-treatment rounds. This lack of sharing does not indicate that non-kin do not form stable sharing bonds. The existence of non-kin bonds is evident from past field and captive studies (Carter & Wilkinson 2013b). In this group, allogrooming and sharing were both more consistent and correlated than expected by chance among non-kin (Appendix 3, Table S4). Rather, these weak levels of sharing stem at least in part from how we paired the limited number of females.

When constructing our experimental dyads, we could not pair every bat with its primary donor. Some bats shared primary donors and bats could not serve in multiple dyads for statistical and logistical reasons (e.g. recovery times for fasting). We therefore paired females with their primary maternal kin donors when they were available. This led to 7 of 8 bats with maternal relatives being paired with their top ranked donor, and only one bat being paired with its second rank donor (its daughter; Appendix 3, Table S1). We formed these dyads first because they provided the reliable and consistent sharing relationships required for testing short-term contingency in a group setting. Since the remaining six females had to be paired with each other, only two were paired with their top ranked donor, three were paired with second ranked donors, and one bat was paired with a low ranked donor (Table S1).

As a consequence, our overall results are driven by mothers and their adult daughters (8 of the 11 subjects we analyzed). This is not, however, ecologically unrealistic, because most of the food sharing among adult vampire bats in the wild occurs between close maternal kin. The bond between adult mother and adult daughter vampire bats is one of the strongest and most common adult relationships in vampire bat social networks, which is consistent with other mammals living in groups with mixed relatedness and female philopatry (e.g. bison: Green 1989, wild boar: Kaminski et al. 2005, giraffes: Bashaw et al. 2007, baboons and other primates: Silk et al. 2006, Seyfarth & Cheney 2012; woodrats: Moses & Millar 1994; elephants: Archie et al. 2006; insectivorous bats: Kerth et al. 2003). In vampires, the frequent sharing within mother and adult daughter bonds makes this relationship a good first place to search for contingency, especially because any contingency found here would indicate a potential interaction between enforcement and kin selection.

Another limitation to this study was that we did not sample allogrooming rates in our targeted pairs during the 6 weeks of experimental fasting trials. It is possible that bats used allogrooming to compensate for a lack of food sharing and to maintain social bonds, as found in primates (Seyfarth & Cheney 1984, de Waal 1997, Gomes & Boesch 2011, Sabbatini et al. 2012 , Fruteau et al. 2009). In vampire bats, this possibility is suggested by correlational network data. For example, during 2010-2014 when considering either all sharing pairs or only related pairs, the best predictor of the amount of food given by A to B is the amount of food A received from B. But when considering only non-kin pairs (kinship <0.05), the best predictor of food given is not food received but rather allogrooming received (Appendix 3, Table S3). This result makes sense if one considers that food sharing, unlike allogrooming, is a relatively rare event with a limited number of donors. Food sharing is inherently dyadic. That is, food given from A to B may decrease food given from A to C, and also decrease food given from C to B. The same is not true for allogrooming: one bat can be groomed simultaneously by two or more conspecifics. From each bat's point of view, this should make allogrooming a more reliable way to maintain social bonds, especially when individuals have multiple social partners.

One clear conclusion is that vampire bat food sharing deviates from many assumptions of models based on 'tit-for-tat' in the iterated prisoner's dilemma (Trivers 1971, Axelrod & Hamilton 1981). These models had a large and important impact on subsequent social evolution theory. Unfortunately, literal translations of the tit-for-tat model have led to experimental predictions that overemphasize isolated single-partner pairs, strict-short-term contingency, and exchanges of a single type of discrete service (reviewed by Carter 2014; Chapter 1). Although these assumptions originally kept the tit-for-tat model simple, they also constrained how experimenters viewed and tested cooperation in later decades (Noë 2006). Increasing evidence suggests enforcement mechanisms can depend crucially on factors missing from the iterated prisoner's dilemma model: partner choice and switching, continuous (i.e.

non-binary) investments, multiple “currencies” (e.g. grooming, food sharing, defense), and long term-social bonds (Carter 2014; Chapter 1).

Reciprocal food sharing in vampire bats was one of the earliest and most convincing examples of reciprocity largely because one part of the study in particular appeared to closely match the features of the tit-for-tat model (Wilkinson 1984). When fasting trials were conducted in a captive sample of unrelated bats with varying co-roosting association, the resulting pattern of 13 food donations was not random; groupmates appeared to pair up and take turns as donor and recipient. This pattern looked like *tit for tat* because it involved pairs contingently exchanging a single service. But our more recent analyses suggest that vampire bats do not show strict short-term contingency within each pair. Furthermore, stable bonds can change when bats are moved from one colony to another (GGC, unpublished data), which shows that partner choice and switching is also possible.

The role of multiple donors has the additional consequence of dividing the total cost of feeding a hungry bat among several donors. In our experiments, even bats that had a mother or daughter present during their observation period, received on average about half of their food from other donors (Figure 11). Non-kin food sharing in vampire bats may therefore be adaptive because it allows bats to maintain a wider social network of donors. This is consistent with the fact that vampire bats that fed more bats, and hence more unrelated bats, had more donors (Appendix 3 Figure S8), and that bats with more partners previously had more donors during the contingency experiment.

Our results do not resolve the controversy over whether vampire bat food-sharing is stabilized by reciprocity. Some models assume that vampire bat food sharing among nonkin simply represents a lack of kin discrimination within a predominantly matrilineal group or a situation where returns on a cooperative investment are ensured by circumstances other than the partner's response (e.g. pseudoreciprocity; see Foster 2004 for a multi-level selection model, see Carter 2014, Chapter 1, for a critical evaluation). According to these models, the marginal costs of sharing small amounts of food may be so low that even consistent individual variation in food sharing cannot result in "subtle cheating" (donors giving consistently less gaining the fitness benefits without paying the same costs). The cost of making food-sharing investments more precise may be greater than the benefit. However, these models provide no testable predictions as to the design of cooperative decisions, so such models must be treated as null hypotheses at best.

A more adaptationist view suggests that bats enforce reciprocal food sharing in a way that is more nuanced and complex than simple tit-for-tat. If a long-term social bond leads to a form of reciprocity with a more complex and robust design, then this would explain why the clearest evidence of short-term contingent reciprocity comes from situations where the cooperating partners lack social bonds (plants and fungi: Kiers et al. 2011; birds on neighboring territories: Godard 1993, Akçay et al. 2009, Krams et al. 2008, 2013; trained rats: e.g. Rutte & Tabosky 2008, Dolivo & Taborksy 2015). And this would explain why evidence for reciprocity has been so ambiguous in species that do have such social bonds (see Chapter 1).

In a long-term cooperative social bond, there are multiple cooperative returns from multiple types of cooperative investments, that may be conceptually reduced to a single measure of relationship quality, i.e. “emotional score-keeping” (e.g. Schino & Aureli 2009, Jaeggi et al. 2012, Seyfarth & Cheney 2012). As a consequence, strict contingencies within each service become less important and obvious. This hypothesis can explain the paradoxical finding that short-term contingency in primates is weakest in strongly bonded partners and strongest in weakly-bonded partners (humans: Shackleford & Buss 1996, other primates: Seyfarth & Cheney 2012). Strong friendships are characterized by diverse social investments and subtle contingency.

Unfortunately, if cooperation in a given species is indeed explained by this more complex model of reciprocity (social bonds with multiple services, long-term contingencies, and a supply and demand of partners), then such cooperative relationships will also be far more difficult to manipulate, and as a consequence, an empirical test of the reciprocity hypothesis is more difficult than often recognized (but see Seyfarth & Cheney 1988). But such tests are not impossible. We suggest that testing the enforcement of cooperation in a complex social network may require experimentally manipulating a single service while measuring multiple responses towards multiple individuals in a group setting that allows partner choice.

In conclusion, vampire bat social bonds may not be strictly contingent in the short-term, perhaps because bats depend on a network of bonded individuals and these bonds likely integrate multiple services, such as allogrooming (Wilkinson 1986) or social thermoregulation (clustering increases with lower temperature: Delpietro &

Russo 2002). Moreover, regurgitated food sharing is a relatively rare event that cannot be induced quickly multiple times in succession. Measuring the role of contingency in vampire bat food sharing will require manipulating and tracking multiple cooperative services (e.g. food sharing, allogrooming, and clustering) in longer-term experiments.

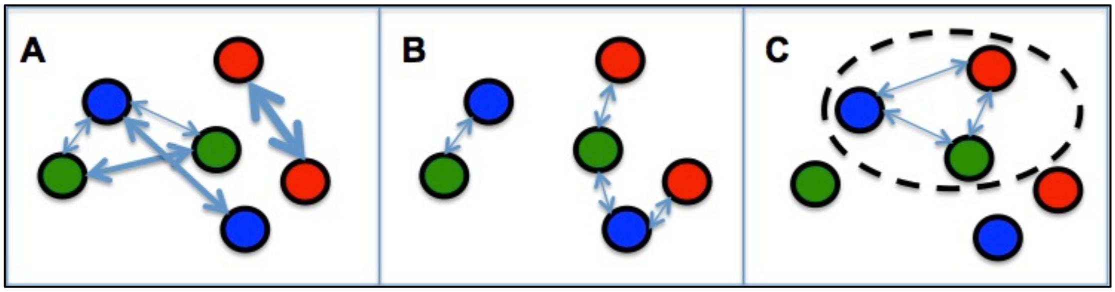


Figure. 6 Three examples of network symmetry without contingency. Nodes are individuals. Arrows are helping behaviors. Panel A: individuals are helping others based on phenotype similarity (color). Panel B: Helping is based on proximity. Panel C: Helping occurs randomly within a small subset of highly bonded individuals.

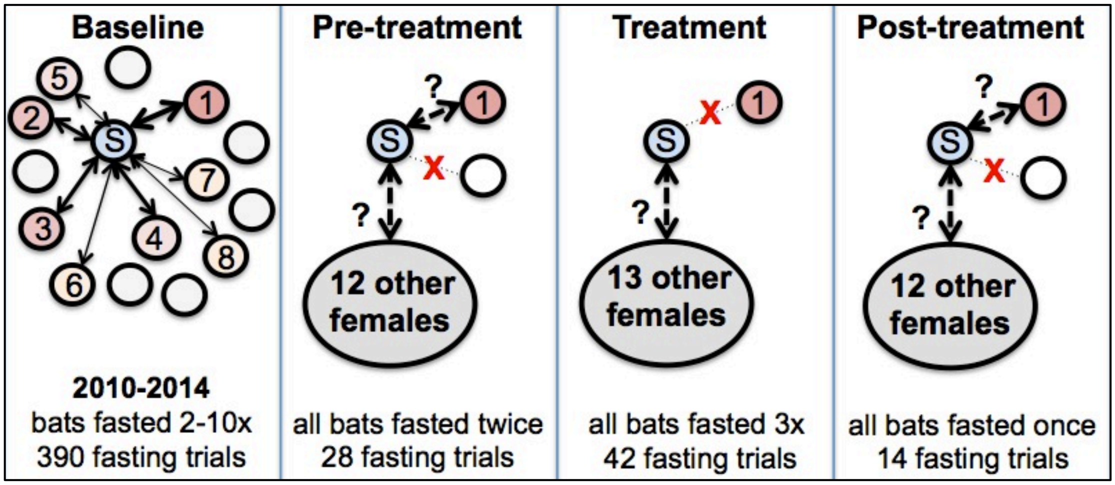


Figure 7. Contingency experiment for a single subject. Circles are bats. Arrows show food given. We first collected baseline data on food-sharing networks from 2010-2014 (mean and median number of donors= 8), then paired 14 subjects (S) with a unique partner that was a consistent and reliable donor (Circle 1). During treatment trials, we prevented reciprocal sharing by simultaneously fasting the subject (bat S) and its primary donor (bat 1). We then measured food given to subject (S) from all other bats. During pre- and post-treatment trials, we simultaneously fasted bats with little or no food-sharing history (S and non-donor), and then measured food given to subject (S) from primary donor (1) and all other bats. Thirteen potential male donors are not shown.

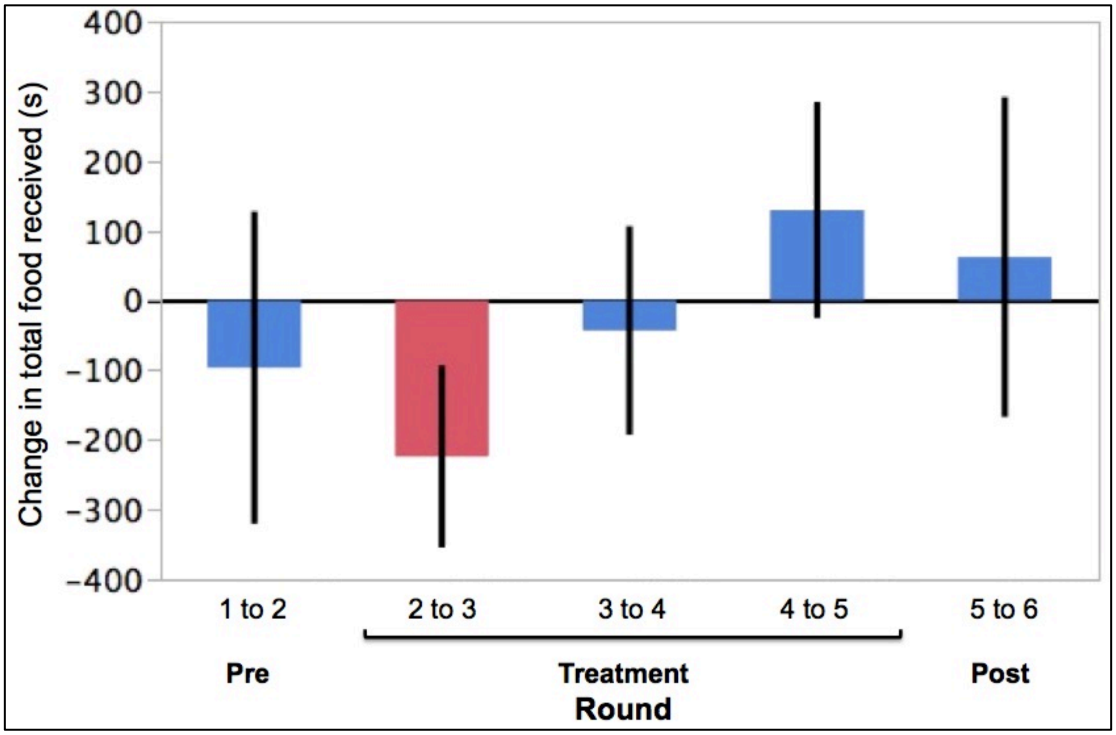


Figure 8. Mean change in total food received between each fasting round. Red bar shows the round when the bat's primary donor was first removed from the donor pool. Error bars are 95% confidence intervals.

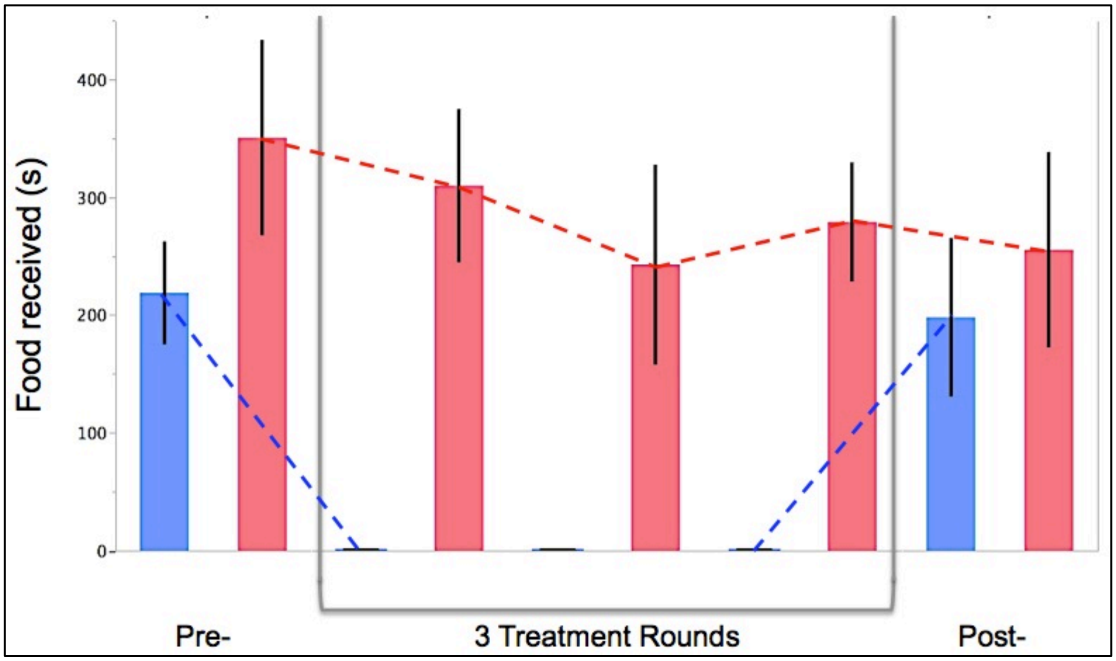


Figure 9. Food received by bats during contingency experiment. Bars show mean food received from targeted primary donor (blue) and all other donors (red) during the pre-treatment, treatment, and post-treatment. Errors bars show standard error of the mean.

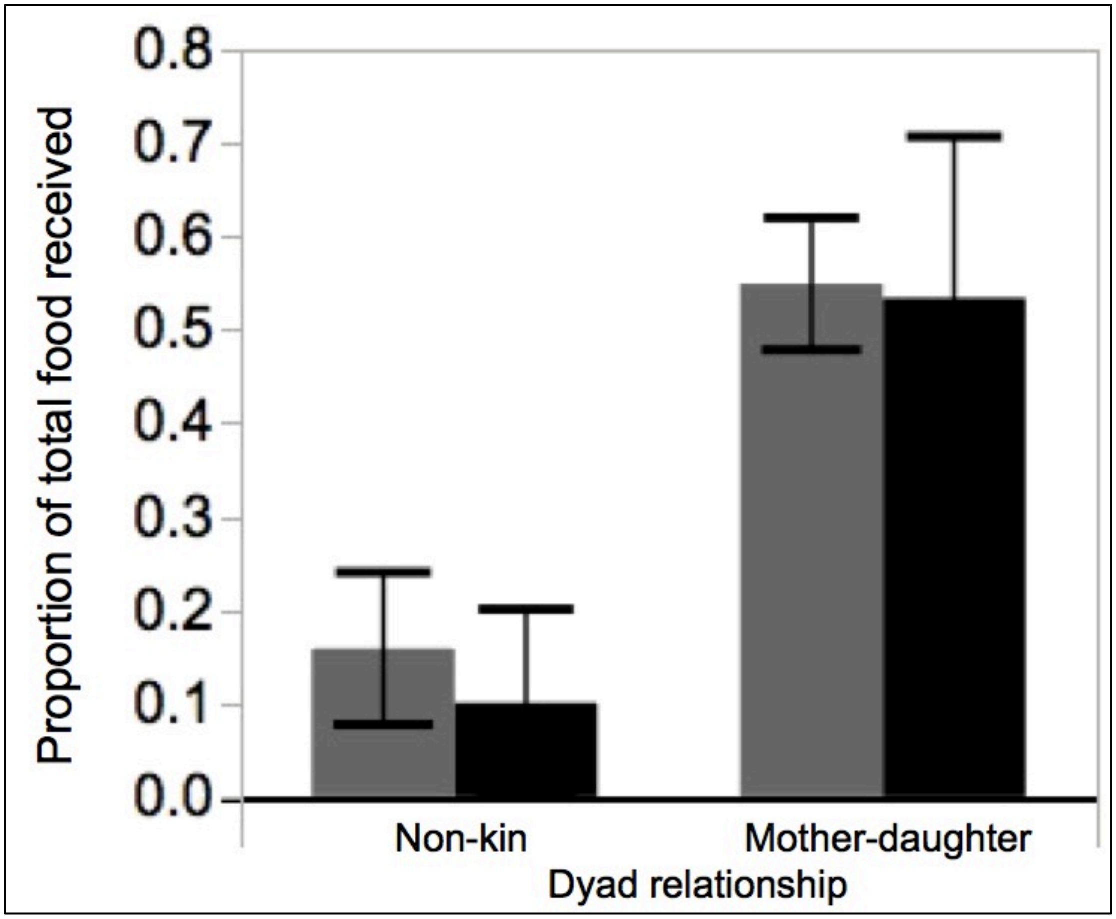


Figure 10. Proportion of food received by kinship. Bars show primary donor's mean percentage contribution to the total food received before (grey) and after (black) the treatment rounds. Means and standard error bars are shown for three non-kin bats, and eight bats whose primary donors were mothers or daughters. We excluded from this graph three bats that did not donate in either the pre- or post-treatment rounds.

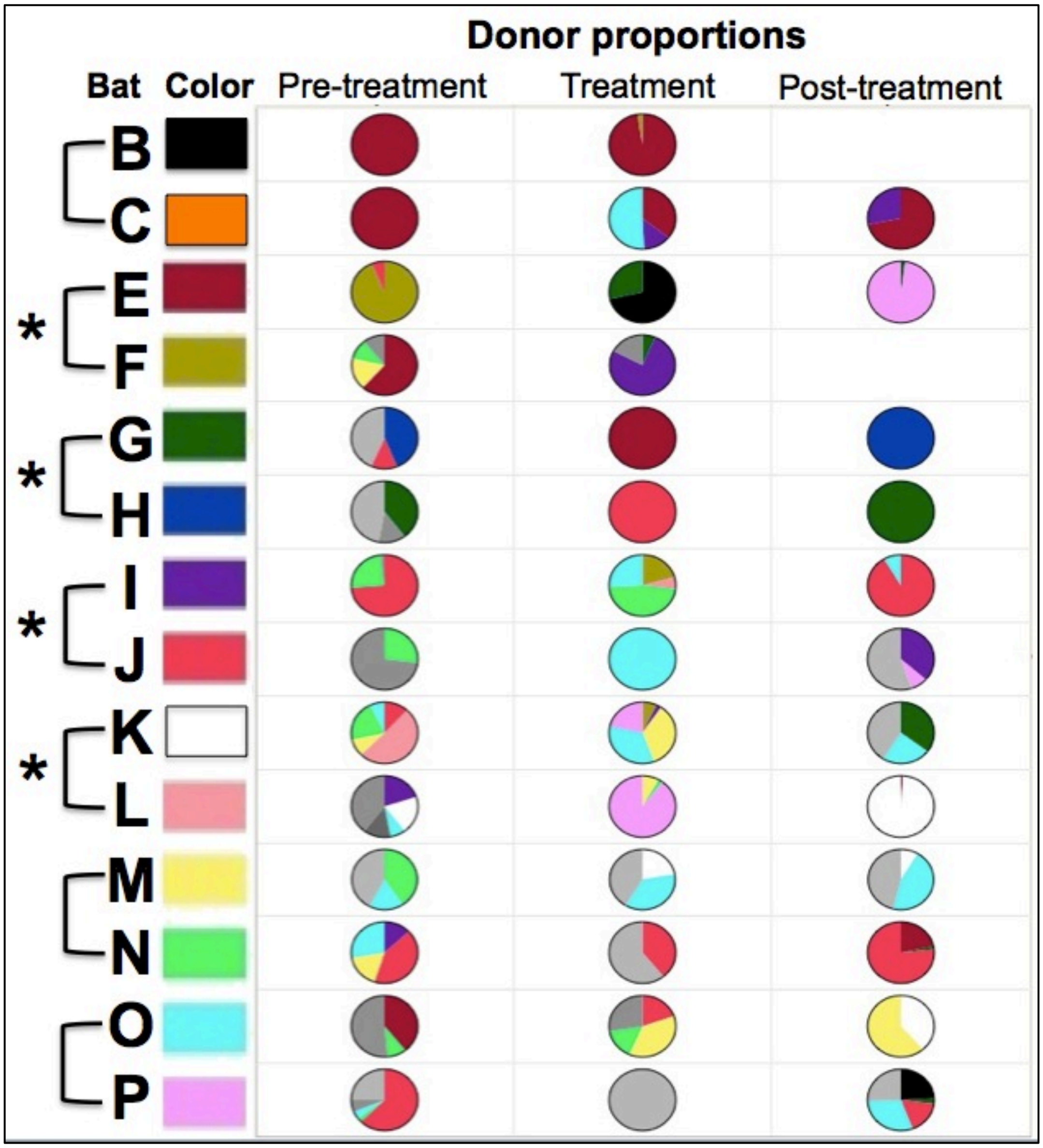


Figure 11. Proportions of food received from each donor. For each female bat (letters), the mean percentage of food received from other females (color) is shown for the first round of each treatment period. Gray shades shows donations from sons (light gray) and other adult males (dark gray). Brackets show experimental pairings. Starred bats are mothers and adult daughters. We excluded bats B, C, and O from the analysis because they were not fed by their paired donors during the pre-treatment rounds.

Appendices

Appendix 1

Selected excerpts from an invited review for *Communicative and Integrative Biology,* "Does food sharing in vampire bats demonstrate reciprocity?" (Carter & Wilkinson 2013b)

… 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 three 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 minute 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.

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 (Wilkinson 1984). 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).

... In the original paper (Carter & Wilkinson 2013a) we used 13 microsatellite loci to estimate kinship, 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 ($\beta=0.07$, $p=0.6$).

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

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

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 & McFarlane (1995)	10	6	Controlled at 100%	No	?
Carter & Wilkinson (2013)	204	25	Controlled at 100%	Not after controlling other factors	Yes

Appendix 2.

Supplement to Chapter 2: *Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment*

Supplement to Methods

We carried out our study in accordance with the *Animal Behavior Society Guidelines for the Use of Animals in Research* (2012), and the Organization for Bat Conservation (Bloomfield Hills, MI, USA).

Microsatellite analysis

We used the web program PRIMER 3 (http://frodo.wi.mit.edu/) to design primers for 12 *Desmodus rotundus* DNA sequences from published repeats (Piaggio et al. 2008) in GenBank, and added 1 additional published microsatellite marker, Tsil3Ca2 (Dechmann et al. 2002). For these 13 microsatellite loci (Carter & Wilkinson 2012), we compared the frequency, and observed and expected heterozygosities from the 25 bats genotyped in our population with 16 free-ranging adult common vampire bats netted in Trinidad, West Indies. We failed to find a significant difference in heterozygosities between observed and expected values (paired t=1.85, n=13, p>0.05) or between the two populations (paired t=1.2, n=13, p>0.05). We used the programs ML-RELATE (Kalinowski et al. 2006) and MICROCHECKER (Van Oosterhout et al. 2004) to check and account for potential scoring errors and null alleles. For 3 loci, we used ML-RELATE to calculate maximum likelihood estimates of the frequency of null alleles for all calculations estimating pairwise relatedness (Kalinowski & Taper 2006).

Sequential analyses

To determine if individual food donations were exchanged in a reciprocal manner over time, we examined the sequence of sharing events across trials. For this analysis we only analysed trials where donors were previously subjects. We also only included mouth-licking bouts longer than 15 s to remove instances of begging. We then tested (1) if the donation size from bat B to bat A in a trial was predicted by the size of the most recent previous donation from A to B, and (2) if the percentage of B's contribution to the total food received by A in a trial was predicted by the percentage of A's contribution to the total food received by B in the most recent previous donation from A to B.

Consistency analysis

To test for evidence of symmetrical and consistent dyadic relationships over time, we examined the amount (food donated/chances to give) and the presence or absence of food sharing for dyads that had multiple chances to donate. We used Mantel and randomization tests to assess similarity of (1) presence and amounts of food sharing in subsequent fasting rounds, (2) presence and amounts of food sharing six months apart, (3) allogrooming given and received within dyads, and (4) the food-sharing matrix with its transpose, using bats that both served as subjects and were available as donors in every round (67% of the total possible food sharing dyads).

Supplement to Results

Pattern of food sharing

We induced food sharing on 48 out of 52 days over a period of 780 days. Overall patterns of food sharing are shown in Figure S2. Female adults and juveniles

(4-8 months old) were always fed by at least one other bat, while 4 of 9 adult males were never fed. After controlling for chances to give and receive, adult females donated 78% and received 57% of the total amount of food donated, while juveniles provided and received an additional 13% and 15% respectively. We observed no food sharing between adult males. However, we did observe two unrelated adult males feeding a male juvenile, and sharing between two unrelated 8 month-old males. Sixty-three of the 98 dyads that shared food had relatedness estimates less than 0.05 (Figure S2). This percentage (64%) is close to the number expected if partners were chosen at random with respect to relatedness because 208 of 312 possible food-sharing dyads (67%) were related by less than 0.05.

Recipients were fed by an average of 3.9 donors in a trial (range=1-7). The median food donated from a donor to recipient in a trial was 191 s (N=204 donations, mean=339 s, range=5-3315 s). When scaling by chances to give, female donors gave food to recipients for an average of 256 s (S.E.=45), and male donors gave for an average of 164 s (S.E.=89). One feeding donation lasting 3315 s from an adult female to a highly related two-year old male was an extreme outlier (Figure S1). The total amount of food received from all donors during the 2 h period was typically about 5% of an adult recipient's mass, which restored ~20% of mass lost during 24 h of fasting. The donation during a trial consisted of several mouth-licking bouts, and the median length of a mouth-licking bout was 40 s (mean=79.9, S.D.=131.6 s).

Predictors of food sharing across dyads

Food received (p<0.0002), donor sex (p<0.0002), and allogrooming received (p=0.0056), but not relatedness (p=0.2896), predicted the presence of food sharing among the 312 dyads where food sharing could have occurred (Figure S4, S5). However, within the subset of 98 dyads that shared food, food donation size was predicted by relatedness ($R^{2=}$0.063, p=0.0032) and food received ($R^{2=}$0.049, p=0.0324) in separate univariate analyses. We found no significant predictors when these factors were considered simultaneously. The effect of relatedness was driven largely by extended maternal care. Mothers feeding their pups or putative subadult offspring (ages 4-31 months) constitute four of the largest donations (Figure S6, three largest outliers in Figure S1). If these dyads are removed, relatedness is no longer a significant predictor (p=0.4).

Appendix 2 Supplementary Figures

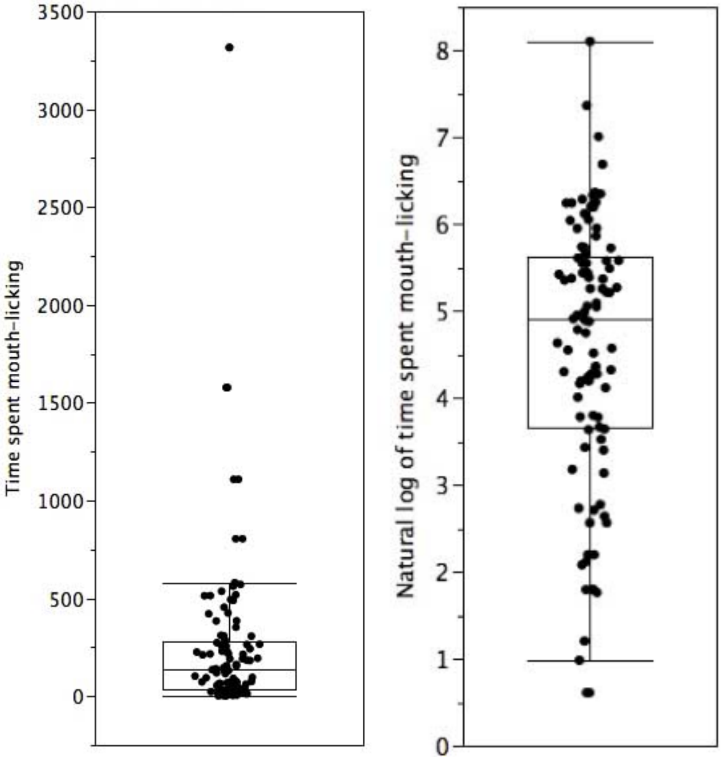
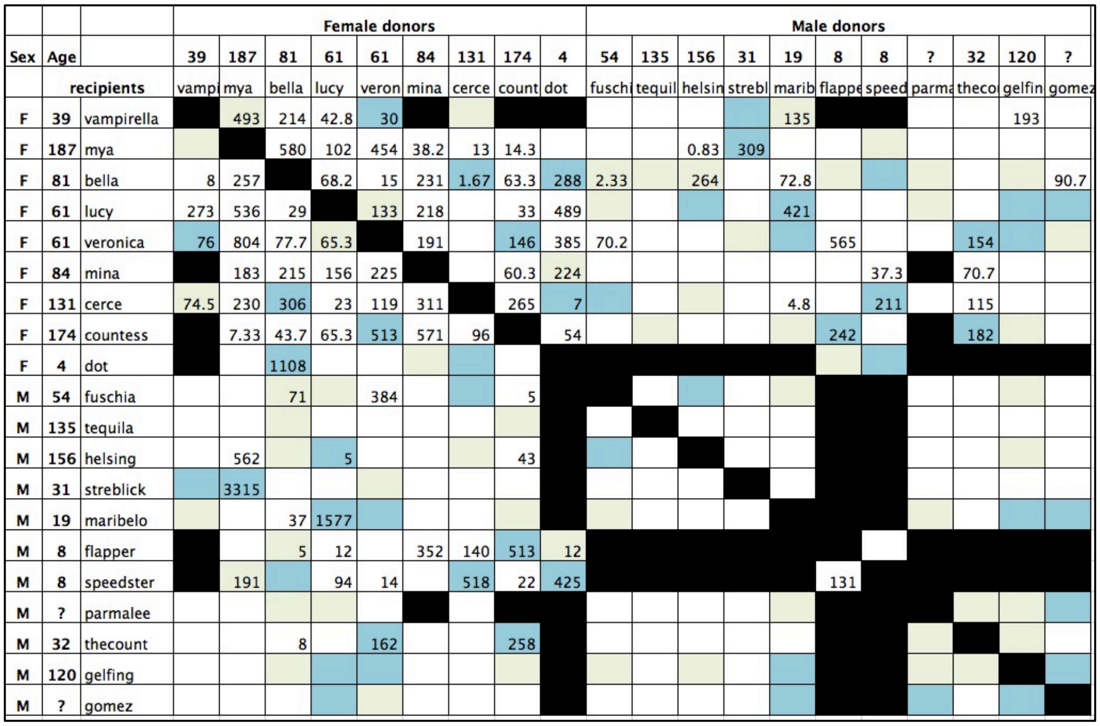


Figure S1. Distribution of mean mouth-licking times before and after log transformation. Mouth-licking time was used to estimate food donated to the subject. Box shows the distance of the interquartile range, the whiskers extend that range 1.5 times, and the line within the box is the median.



			Female donors									Male donors										
Sex	**Age**		**39**	**187**	**81**	**61**	**61**	**84**	**131**	**174**	**4**	**54**	**135**	**156**	**31**	**19**	**8**	**8**	**?**	**32**	**120**	**?**
		recipients	vampi	mya	bella	lucy	veron	mina	cerce	count	dot	fuschi	tequil	helsin	strebl	marib	flappe	speed	parma	theco	gelfin	gomez
F	**39**	vampirella		493	214	42.8	30									135					193	
F	**187**	mya			580	102	454	38.2	13	14.3				0.83	309							
F	**81**	bella	8	257		68.2	15	231	1.67	63.3	288	2.33		264		72.8						90.7
F	**61**	lucy	273	536	29		133	218		33	489					421						
F	**61**	veronica	76	804	77.7	65.3		191		146	385	70.2					565			154		
F	**84**	mina		183	215	156	225			60.3	224							37.3		70.7		
F	**131**	cerce	74.5	230	306	23	119	311		265	7					4.8		211		115		
F	**174**	countess		7.33	43.7	65.3	513	571	96		54						242			182		
F	**4**	dot			1108																	
M	**54**	fuschia			71		384			5												
M	**135**	tequila																				
M	**156**	helsing		562		5				43												
M	**31**	streblick		3315																		
M	**19**	maribelo			37	1577																
M	**8**	flapper			5	12		352	140	513	12											
M	**8**	speedster		191		94	14		518	22	425						131					
M	**?**	parmalee																				
M	**32**	thecount			8		162			258												
M	**120**	gelfing																				
M	**?**	gomez																				

Figure S2. Food donated values shown as a sociomatrix. Columns are donors and rows are fasted subjects. Blank squares have zero values and black squares are dyads that did not have an opportunity to donate or receive food. Dyads are coloured according to estimates of pairwise relatedness (r): white for r estimates 0—0.05, light green for r estimates between 0.05—0.25, and blue for r estimates >0.25. Numbers are mean seconds of food sharing per trial. Unit for age is months.

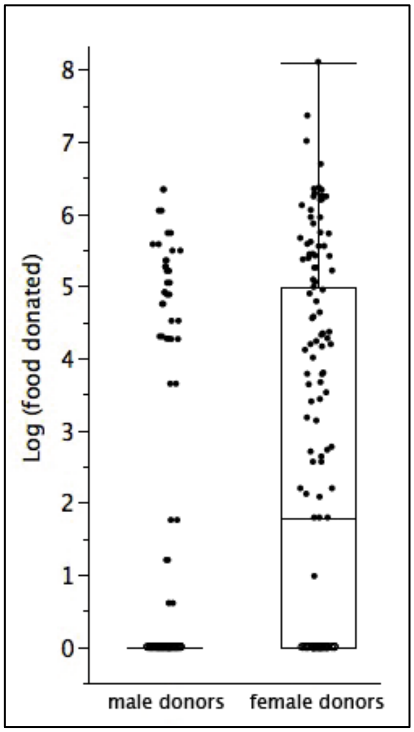


Figure S3. Box plot showing food donated by donor sex. Box shows the distance of the interquartile range, the whiskers extend that range 1.5 times, and the line within the box is the median.

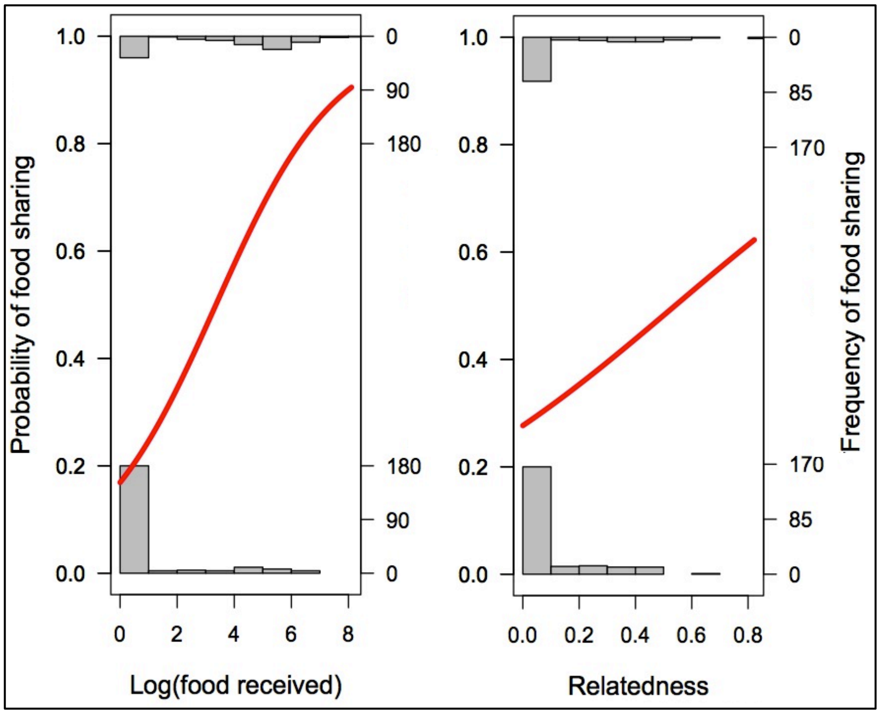


Figure S4. Logistic regression plot. The effect of log food received and relatedness on the presence of food sharing is shown.

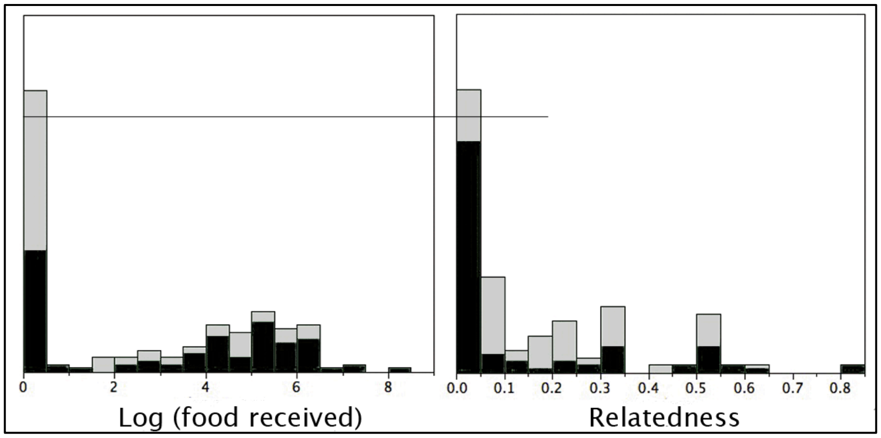


Figure S5. Frequency histograms showing proportion of dyads that shared food across values of food received and relatedness. Grey bars show dyads that could have shared food in both directions and black bars show dyads that did share food. Length of bars above horizontal line is reduced by 95% to fit graph (length is equally reduced above line for both histograms).

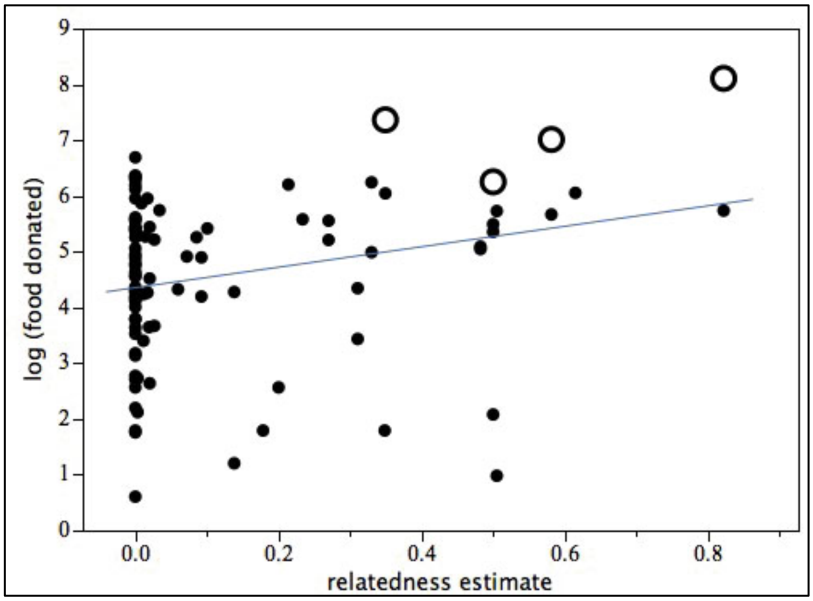


Figure S6. Relationship between relatedness and food donated. Values for mothers feeding juvenile or putative adult offspring are shown as open circles.

Appendix 3

Supplement to **Chapter 3: Intranasal oxytocin increases social grooming and food sharing in the common vampire bat *Desmodus rotundus***

Additional allogrooming experiment with young males. We tested each of 12 young males (ages 4-23 months) by treating them with OT or saline as described above, then placing them with their mothers in a smaller (0.3 x 0.4 x 0.5 m) plexiglass cage. We video recorded this caged dyad for 1 hour on 2 different days at the same hour (1700 or 1800h) with a Sony Nightshot camera and infrared spotlight. Observers that were blind to the treatment scored the seconds of allogrooming given and received by the unmarked male. We detected no effect on allogrooming given (Wilcoxon Signed rank test, S=5.5, p=0.72), received (S=3,p=0.34), total allogrooming (S=3.5, p=0.62) or physical contact (S=9, p=0.26).

Appendix 4

Supplement to **Chapter 4: Vampire bats do not play strict 'tit for tat' when sharing food**

Table S1. Directional dyads selected for contingency experiment

Subject bat	**'Primary donor'**	**Subject's relationship**	**Primary's donor rank**[1]	**Partner kinship (r)**	**Subject age (y)**
B*	C	Unknown	1	0.4	12
C*	B	Unknown	2 (1=A)	0.4	7
E	F	Mother of F	1	0.5	13
F	E	Daughter of E	1	0.5	1.5
G	H	Mother of H	1	0.5	9
H	G	Daughter of G	1	0.5	3
I	J	Mother of J	1	0.5	17
J	I	Daughter of I	1	0.5	1.5
K	L	Mother of L	2 (1=M)	0.5	8
L	K	Daughter of K	1	0.5	2
M	N	Unknown	2 (1=G)	0	18
N	M	Unknown	2 (1=O)	0	8
O*	P	Unknown	9 (1=N)	0	9
P	O	Unknown	1	0	6

1. Food received rank among all subject's female donors from high to low. *excluded from analysis (see results).

Table S2. Polymorphic microsatellite loci

Label	Seq	TempM	HW-p	Motif	Product (sizes)
Dr1-1	1	60.1/59.1	0.03	(CT)25;(CA)23	10 (124-170)
Dr2-2	1	60.3/60.0	0.55	(CA)11	6 (161-173)
Dr3-3	1	60.0/60.7	NA	(CA)8	1 (145)
Dr4-4	1	60.4/59.8	0.56	(GA)9	9 (144-184)
Dr5-5	1	60.4/59.0	0.04	(CT)6	2 (114-116)
Dr6-6	1	59.9/59.9	0.11	(CA)21	8 (132-151)
Dr7-7	1	59.8/57.4	0.0022	(GA)21	6 (138-160)
Dr8-8	1	60.6/60.0	0.25	(GT)9	7 (147-161)
Dr9-9	1	59.9/60.5	0.052	(CA)17	8 (128-152)
Dr10-10	1	60.1/60.8	0	(GT)7;(GA)20	8 (143-194)
Dr 11-11	1	59.2/60.1	0.0062	(GA)18	6 (151-174)
Dr12-12	1	60.1/60.0	0.0014	(GT)15	3 (117-132)
Dr13-Ts9	2	60.0/60.0	0.0014	(GT)21	10 (177-207)
Dr14-14	3	59.1/58.4	0.27	(CA)12	5 (223-235)
Dr15-15	3	58.9/58.0	0.084	(CA)11	8 (199-218)
Dr16-16	3	58.1/59.0	0.002	(CA)13	7 (179-195)
Dr17-17	3	58.0/59.1	0	(GT)20	6 (175-189)
Dr18-18	3	57.0/58.9	0.25	(GT)10	4 (196-206)
Dr19-19	3	58.3/59.2	0	(GT)13, (GT)4	3 (176-189)
Dr20-23	3	60.7/59.0	0.0002	(TATC)9;(TC)19	3 (121-152)
Dr21-28b	3	59.4/58.4	0.94	(CA)8	3 (128-134)
Dr22-32	3	58.7/58.6	0	(CT)8;(CT)5	4 (232-245)*
Dr23-35	3	60.7/59.8	0	(CA)20	6 (173-187)*
Dr24-02	3	60.4/58.2	0.56	(AGC)8	2 (143-149)
Dr25-c7	4	61.7/62.0	0.084	(AATG)6	4 (236-247)
Dr26-dr1	5	59.9/59.6	0.91	(AAAC)9	5 (109-123)*
Dr27-dr7	5	56.0/57.4	0	(AATG)6	6 (163-181)*
Dr28-dr9	6	58.4/60.3	0.85	(CA)9	5 (120-126)
Dr29-dr12	6	59.9/59.2	0.43	(GA)8	2 (212-216)
Dr30-dr15	6	60.7/60.1	0.44	(AGAT)12	8 (145-203)
Dr31-dr17	6	60.1/60.4	0.52	(CA)13	5 (159-209)

Seq= Sequence Source: (1) Piaggio et al. 2008: GenBank Accession # EF591569–EF591580; (2) Dechmann et al. 2002: GenBank Accession # AF431030; (3) GenBank Accession # PRJNA279293 (DR_1); (4) McCulloch & Stevens 2011: AL2_27850; (5) GenBank Accession # PRJNA279293 (DR_2);(6) GenBank Accession # PRJNA279293 (DR_3); **HW-p**= p-value for Hardy-Weinberg test of heterozygote deficiency (low=below expected). **TempM**= melting temperature of L/R primer (Table S3); **Motif**= type and number of repeats in source sequence; **Product**= number of products in captive study group (observed size range). *indicates presence of null alleles detected and assumed for calculations.

Table S3. Microsatellite primer sequences

Label	Left primer sequence (5' to 3')	Right primer sequence (5' to 3')
Dr1-1	CATCACACGTCTTTCCATGC	GGCCAAACTAATACATTAACTAAGAGG
Dr2-2	GGCAAGTTGGGAGAGTTCCT	AGACTCGCCATCTCCTGAAA
Dr3-3	CAGGACAGGATACATCGTGAAA	TGCGTGTTGTTGTGTAGTGATG
Dr4-4	CACCTCCACTTAACATTTCTCC	TCCTCCTTCCTTCCTTCCTC
Dr5-5	CTTGGCCTTCACAAAGCAGT	TTGTTTTAATGCCCTTTTTGG
Dr6-6	TCCATCTTGATGGGAACCTC	ACCTTCAACCCCACTCACAC
Dr7-7	CCCTGTCTCTGCCTTCATTC	TTGTAAGTTGTTAACCGTTTTCC
Dr8-8	GGCCTAGGGCAAGAATGAGT	CACGATGCACCCACAGATAC
Dr9-9	CTCCTGCTGGGTCACCTAAG	TATGACGGATGCATGTGAGG
Dr10-10	CAGAGTGCATTTGGCTCTGA	CAAGGCCGATAGTCGTTGAG
Dr 11-11	CCCATCGTGCATACTGAAAG	ACACCGTCTCTTGCTCTTGC
Dr12-12	TTAAGTCCACTGCCCCAGAC	TTCCTGGTTACTCCCTGTGG
Dr13-Ts9	TGGCACCACTTTCTTGTCAG	TGGTGGTGGTCACAGGAATC
Dr14-14	CAGCAAATGACTCAGCAGCA	TGCCCTGTCTAACGATCACT
Dr15-15	ACCCAAGTGCCCATAGACAA	TGGTCCAGTGTATCTTAAATCGG
Dr16-16	AGTCCCATATTCAGCCCTGT	TTTGTCTCCCTTTGCTTGCC
Dr17-17	CTGACTGGGAATCGAACTGG	ACATGCACCATTGAGCTGTG
Dr18-18	AGTTAGTGTGCCAGCGAG	TCACACCCACTGCTCTCAAT
Dr19-19	ACAAGAAAAGGGGAAGGTGTG	TCACTGCTGCTTCTTGACCT
Dr20-23	CTGAGAGGGGCCGGTTCT	GTCGTAGTGTAGTGTGTGTGTG
Dr21-28b	AGCCAACACTGACATGCAC	GGGTGTATGTGTAGACGTGC
Dr22-32	ATATCTTCCCATCCGAGGCC	TCTTCCTGGTTCTATGTTGGAGA
Dr23-35	CTGACTGGGAATCGAACTGG	CATGCACCATTGAGCTGTG
Dr24-02	TTGTGTGAGAAGCTCCCAGG	GGGACTACACTTCTTTCCCTC
Dr25-c7	TCCACAGCTAAGGGACTAACCC	TGGCCTTTCAATTACACCCC
Dr26-dr1	GAGTGCAAACGTCCTAACCAG	CATTGTGTCAGGCAGGAGTG
Dr27-dr7	ATCTCACGTAATGCTGACAG	TGACAAACGCAGATCTGATTC
Dr28-dr9	TTCACGCATGGACTTCTACC	ACGGACCGAGAGAGAAATCAC
Dr29-dr12	CCACTCAGGTCTCCGTACTG	AACTGATCAGCGTGTTTCCC
Dr30-dr15	ACCTCTGCCATTGGTCAAGG	GCTGTGCAACTATCACCATCC
Dr31-dr17	AAGCACCATTTCCACTTGCC	GTTGATGGATGCACGCTGAG

Analysis of food sharing 2010-2014

To test the relative importance of social factors in a multivariate model for food given among dyads, we z-transformed all variables and then entered food received, grooming received, kinship, donor sex and subject sex (encoded as dummy variables) into a backward stepwise regression using AIC in JMP 11. After removing variables, we then re-tested the remaining variables and all possible interactions using the more restrictive Bayesian Information Criterion for model simplicity. To test this model, we permuted food donated to sets of predictor variables using the lmp function in the R package lmPerm (see Carter & Wilkinson 2013 for more detail). We ran 10,000,000 permutations to ensure stable p-values.

For dyads of known pedigree relationship, we replaced the relatedness estimates from genotyping data with the appropriate kinship level (0.5 for parent-offspring, and full sibs, 0.25 for half-sibs, etc). The original and adjusted values were highly correlated (r= 0.92), and we used the pedigree-adjusted values in our model because, for explaining variation in food given, the adjusted values (R^2=0.16) outperformed the original kinship estimates (R^2=0.14). We re-tested the model with subsets of kin (>0.05) and non-kin (<0.05) dyads to interpret kinship interactions.

Permutation tests on our final model revealed that food given was predicted by food received, grooming received, the interaction between food received and kinship, and donor sex (Table S4). Among kin dyads, food given was predicted by food received with an effect that increased with kinship; however, among non-kin dyads, food given was best predicted by grooming received (Table S4).

Table S4. Predictors of food given

	All sharing dyads[1] N=442		Kin dyads[2] N=156		Non-kin dyads[3] N=286	
Predictors	coefficient	P	coefficient	P	coefficient	P
food received	0.35	0.0022	0.44	0.0086		NS
grooming received	0.24	0.016	0.11	NS (0.067)	1.45	0.0001
food received & kinship interaction	0.16	0.0001	0.19	0.017		NS
donor sex	0.11	0.0029		NS		NS
grooming & kinship interaction		NS		NS		NS
kinship		NS		NS		NS

1. adjusted R^2=0.56, F(6,339)=74.0, p<0.0001; 2. Kinship>0.05, adjusted R^2=0.68, F(6,117)=45.4, p<0.0001; 3. Kinship<0.05, adjusted R^2=0.35, F(6,215)=20.97, p<0.0001

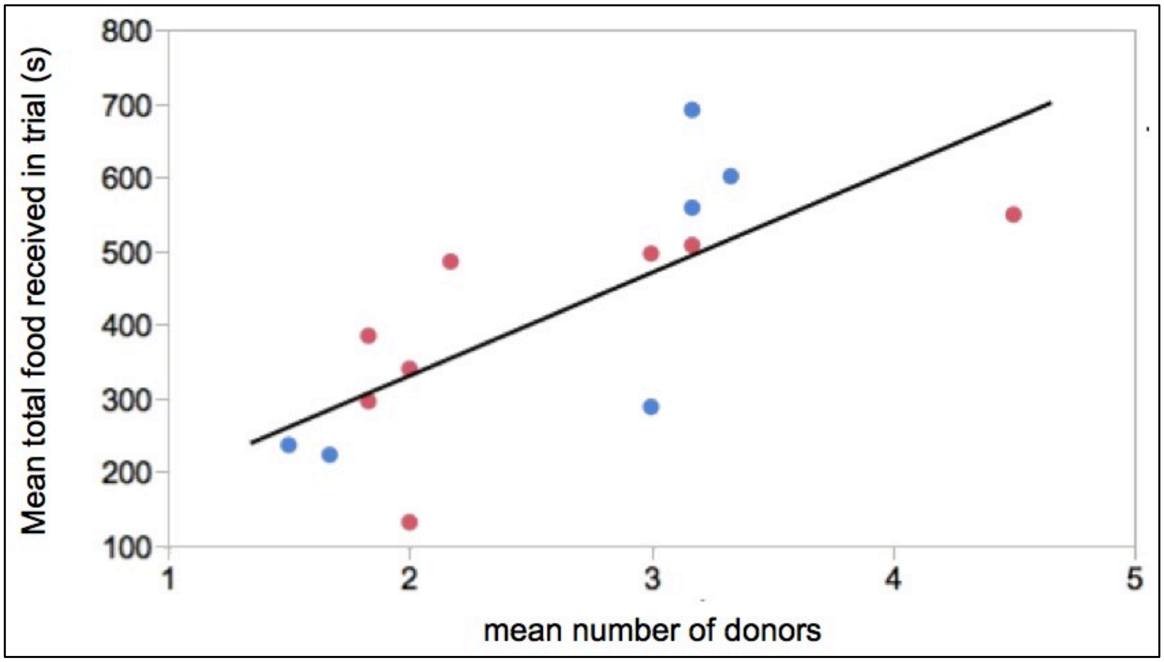


Figure S7. Females with more donors received more food in the contingency experiment. Means were calculated across all rounds for each bat, including eight females with matrilineal kin (red) and six other females (blue).

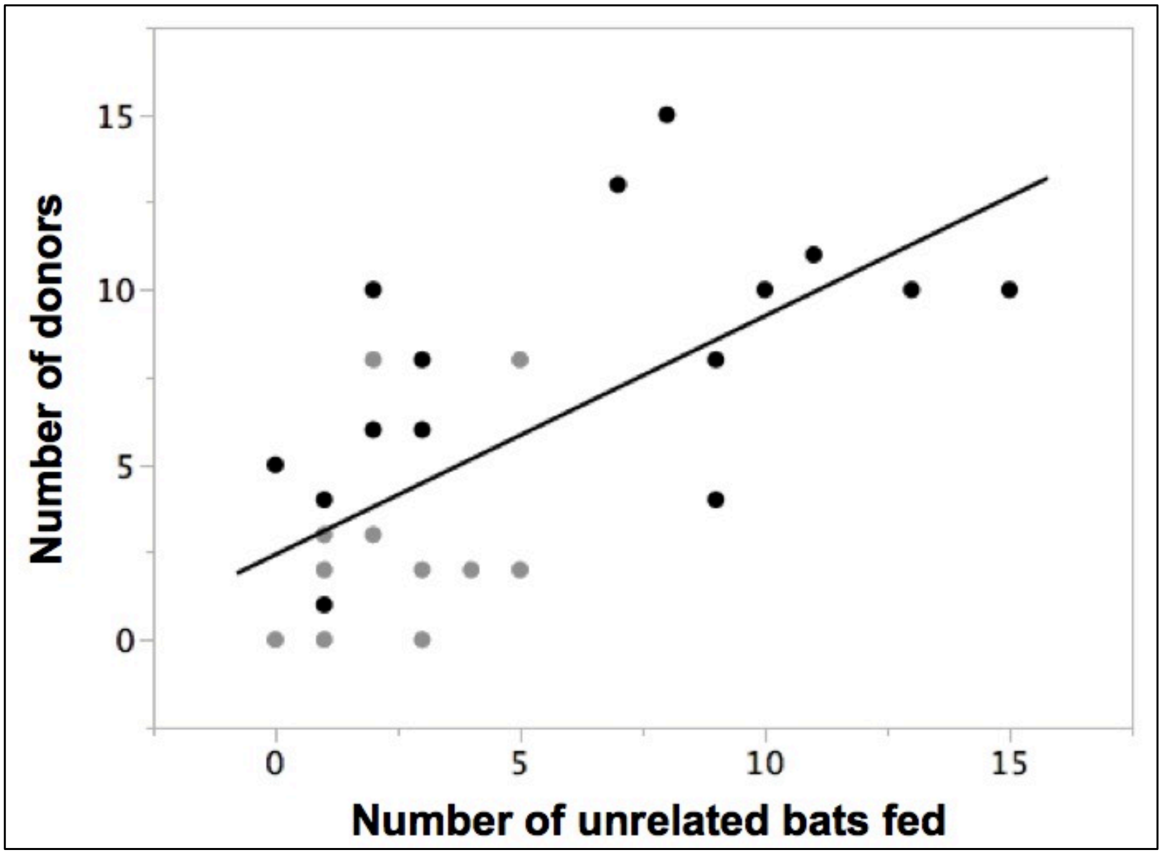


Figure S8. Bats that fed more unrelated bats had more donors. Data based on 2010-2014 food sharing network including 15 females (black) and 11 males (grey). R^2=0.44, permutation p<0.0002.

References

Abric, J. C., & Kahan, J. P. (1972). The effects of representations and behavior in experimental games. *European Journal of Social Psychology*, *2*, 129-144.

Akçay, Ç., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E., & Beecher, M. D. (2009). Good neighbour, bad neighbour: Song sparrows retaliate against aggressive rivals. *Animal Behaviour*, *78*, 97-102.

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, *5*, 325-383.

André, J. B. (2014). Mechanistic constraints and the unlikely evolution of reciprocal cooperation. *Journal of Evolutionary Biology*, *27*, 784–795.

Archie, E. A., Moss, C. J., & Alberts, S. C. (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 513-522.

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390-1396.

Bartz, J. A., Zaki, J., Bolger, N., Ochsner, K. N. (2011). Social effects of oxytocin in humans: context and person matter. *Trends in Cognitive Sciences,* 15, 301-309.

Bashaw, M. J., Bloomsmith, M. A., Maple, T. L., & Bercovitch, F. B. (2007). The structure of social relationships among captive female giraffe (*Giraffa camelopardalis*). *Journal of Comparative Psychology*, *121*, 46.

Bateson, M., Nettle, D., & Roberts, G. (2006). Cues of being watched enhance cooperation in a real-world setting. *Biology Letters*, *2*, 412-414.

Bednekoff, P. A., Balda, R. P., Kamil, A. C., & Hile, A. G. (1997). Long-term spatial memory in four seed-caching corvid species. *Animal Behaviour*, *53*, 335-341.

Bergmüller, R., Johnstone, R. A., Russell, A. F., & Bshary, R. (2007). Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes*, *76*, 61-72.

Boster, F. J., Rodriguez, J. I., Cruz, M. G., & Marshall, L. (1995). The relative effectiveness of a direct request message and a pregiving message on friends and strangers. *Communication Research*, *22*, 475-484.

Box, G. E. P., & Draper, N. R. (1987). *Empirical model-building and response surfaces*, John Wiley & Sons, New York, NY. ISBN 0-471-81033-9.

Brosnan, S. F., Silk, J. B., Henrich, J., Mareno, M. C., Lambeth, S. P., & Schapiro, S. J. (2009). Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Animal Cognition*, *12*, 587-597.

Brown, J. L. (1983). Cooperation: A biologist's dilemma. *Advances in the Study of Behavior*, *13*, 1-37.

Bshary, R. (2010). Cooperation between unrelated individuals – a game theoretic approach. In P. M. Kappeler (Ed.), *Animal Behaviour: Evolution and Mechanisms* (p. 213-240). Germany: Springer Berlin Heidelberg.

Bshary, R., & Grutter, A. S. (2002a). Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: The cleaner fish case. *Ecology Letters*, *5*, 130-136.

Bshary, R., & Grutter, A. S. (2002b). Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Animal Behaviour*, *63*, 547-555.

Bshary, R., & Grutter, A. S. (2005). Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters*, *1*, 396-399.

Bshary, R., & Grutter, A. S. (2006). Image scoring and cooperation in a cleaner fish mutualism. *Nature*, *441*, 975-978.

Bshary, R., Grutter, A. S., Willener, A. S., & Leimar, O. (2008). Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature*, *455*, 964-966.

Burton-Chellew, M. N., & West, S. A. (2012). Pseudocompetition among groups increases human cooperation in a public-goods game. *Animal Behaviour*, *84*, 947-952.

Burton-Chellew, M. N., & West, S. A. (2013). Prosocial preferences do not explain human cooperation in public-goods games. *Proceedings of the National Academy of Sciences*, *110*, 216-221.

Calcagnoli, F., Kreutzmann, J. C., de Boer, S. F., Althaus, M., Koolhaas, J. M. (2015). Acute and repeated intranasal oxytocin administration exerts anti-aggressive and pro-affiliative effects in male rats. *Psychoneuroendocrinology, 51*, 112-121.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, *106*, 13850-13853.

Carter, G. (2014). The reciprocity controversy. *Animal Behavior and Cognition*, 1, 368-386. doi: 10.12966/abc. 08.11. 2014.

Carter, G. G. & Wilkinson, G. S. (2012). Data from: Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Dryad Digital Repository*. doi:10.5061/dryad.tg7b1.

Carter, G. G., & Wilkinson, G. S. (2013a). Food sharing in vampire bats: Reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122573.

Carter, G., & Wilkinson, G. (2013b). Does food sharing in vampire bats demonstrate reciprocity? *Communicative & Integrative Biology*, *6.*, e25783.

Carter, G. G., & Wilkinson, G. S. (2013c). Cooperation and conflict in the social lives of bats. In R. A. Adams, & S. C. Pedersen (Eds.) *Bat evolution, ecology, and conservation* (p. 225-242). New York, NY: Springer.

Carter, G. G., Skowronski, M. D., Faure, P. A., & Fenton, B. (2008). Antiphonal calling allows individual discrimination in white-winged vampire bats. *Animal Behaviour*, *76*, 1343-1355.

Carter G., Logsdon, R., Arnold, B, Menchaca, A., Medellin, R. 2012. Adult vampire bats produce contact calls when isolated: acoustic variation between species, colonies, and individuals. *PLOS One*. 7: e38791. doi:10.1371/journal.pone.0038791.

Cheney, D. L. (2011). Extent and limits of cooperation in animals. *Proceedings of the National Academy of Sciences*, *108*, 10902-10909.

Clark, M. S., & Mills, J. (1979). Interpersonal attraction in exchange and communal relationships. *Journal of Personality and Social Psychology*, *37*, 12.

Clements, K. C. & Stephens, D. W. (1995) Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. *Animal Behaviour*, *50*, 527-535.

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*, 51-57.

Connor, R. C. (1986). Pseudo-reciprocity: Investing in mutualism. *Animal Behaviour*, *34*, 1562-1566.

Connor, R. C. (1992). Egg-trading in simultaneous hermaphrodites: an alternative to Tit-for-Tat. *Journal of Evolutionary Biology*, *5*, 523-528.

Connor, R. C. (1995a). Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma.' *Trends in Ecology & Evolution*, *10*, 84-86.

Connor, R. C. (1995b). Impala allogrooming and the parcelling model of reciprocity. *Animal Behaviour*, *49*, 528-530.

Connor, R. C. (1996). Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Animal Behaviour*, *51*, 451-454.

Connor, R. C. (2010). Cooperation beyond the dyad: On simple models and a complex society. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2687-2697.

Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, *31*, 187-276.

Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. H. Barkow, L. E. Cosmides, & J. E. Tooby, (Eds). *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (p. 163-228). Oxford, UK: Oxford University Press.

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B*. 280, 20122765.

Crockford, C., Deschner, T., Ziegler, T. E., Wittig, R. M. (2014). Endogenous peripheral oxytocin measures can give insight into the dynamics of social relationships: a review. *Fronters in Behavioral Neuroscience* 8, 68.

Croft, D. P., James, R., Thomas, P. O. R., Hathaway, C., Mawdsley, D., Laland, K. N., & Krause, J. (2006). Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, *59*, 644-650.

Darwin, C. (1859). *On The Origin of Species by Means of Natural Selection*. John Murray, London.

Davies, N.B., Krebs, J.R., West, S.A. (2012). *An Introduction to Behavioural Ecology*, 4th edn. Oxford, UK: Wiley-Blackwell.

Dechmann, D., Garbely, E., Kerth, G. & Garner, T. (2002). Highly polymorphic microsatellites for the study of the round-eared bat, *Tonatia silvicola* (d'Orbigny). *Conservation Genetics, 3*, 455–458.

Delton, A. W., Krasnow, M. M., Cosmides, L., & Tooby, J. (2011). Evolution of direct reciprocity under uncertainty can explain human generosity in one-shot encounters. *Proceedings of the National Academy of Sciences USA*, *108*, 13335-13340.

Delpietro, V. H., & Russo, R. G. (2002). Observations of the common vampire bat (*Desmodus rotundus*) and the hairy-legged vampire bat (*Diphylla ecaudata*) in captivity. *Zeitschrift für Säugetierkunde*, *67*, 65-78.

DeNault, L. K., & McFarlane, D. A. (1995). Reciprocal altruism between male vampire bats, Desmodus rotundus. *Animal Behaviour*, *49*, 855-856.

Denison, R. F. (2000). Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *The American Naturalist*, *156*, 567-576.

de Waal, F. B. (1997). The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, *18*, 375-386.

de Waal, F. B. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, *60*, 253-261.

de Waal, F. B. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology*, *59*, 279-300.

de Waal, F. B., & Brosnan, S. F. (2006). Simple and complex reciprocity in primates. In P. M. Kappeler, & C. P. van Shaik (Eds.) *Cooperation in primates and humans* (p. 85-105). Germany: Springer Berlin Heidelberg.

de Waal, F., & Luttrell, L. M. (1988). Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*, *9*, 101-118.

de Waal, F. B., & Suchak, M. (2010). Prosocial primates: Selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2711-2722.

Diggle, S. P., Griffin, A. S., Campbell, G. S., & West, S. A. (2007). Cooperation and conflict in quorum-sensing bacterial populations. *Nature*, *450*, 411-414.

Doebeli, M., & Hauert, C. (2005). Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecology Letters*, *8*, 748-766.

Dolivo, V. & Taborsky, M. (2015). Norway rats reciprocate help according to the quality of help they received. *Biology Letters*, *11*, 20140959.

Dugatkin, L. A. (1988). Do guppies play TIT FOR TAT during predator inspection visits? *Behavioral Ecology and Sociobiology*, *23*, 395-399.

Dugatkin, L. A. (1991). Predator inspection, tit-for-tat and shoaling: A comment on Masters & Waite. *Animal Behaviour*, *41*, 898-899.

Dugatkin, L. A. (1997). *Cooperation among animals: An evolutionary perspective*.. Oxford, UK: Oxford University Press.

Dugatkin, L. A., & Alfieri, M. (1991). Guppies and the TIT FOR TAT strategy: Preference based on past interaction. *Behavioral Ecology and Sociobiology*, *28*, 243-246.

Dugatkin, L. A., & Alfieri, M. (1992). Interpopulational differences in the use of the tit-for-tat strategy during predator inspection in the guppy, *Poecilia reticulata*. *Evolutionary Ecology*, *6*, 519-526.

Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity after all: Computation behind token transfers in orang-utans. *Biology Letters*, *5*, 172-175.

Dunbar, R. I., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*, 1344-1347.

Dunbar, R. I., & Shultz, S. (2010). Bondedness and sociality. *Behaviour*, *147*, 775-803.

Fischer, E. A. (1984). Egg trading in the chalk bass, *Serranus tortugarum*, a simultaneous hermaphrodite. *Zeitschrift für Tierpsychologie*, *66*, 143-151.

Foster, K. R. (2004). Diminishing returns in social evolution: the not-so-tragic commons. *Journal of Evolutionary Biology, 17*, 1058–1072. doi:10.1111/j.1420-9101.2004.00747.x

Foster, K. R., & Kokko, H. (2006). Cheating can stabilize cooperation in mutualisms. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 2233-2239.

Foster, K. R., & Wenseleers, T. (2006). A general model for the evolution of mutualisms. *Journal of Evolutionary Biology*, *19*, 1283-1293.

Fraser, O. N., & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. *Animal Behaviour*, *83*, 171-177.

Frank, R. H. (1988). *Passions Within Reason: The Strategic Role of the Emotions*. New York, NY: WW Norton & Co.

Frank, S. A. (1995). Mutual policing and repression of competition in the evolution of cooperative groups. *Nature*, *377*(6549), 520-522.

Fruteau, C., Voelkl, B., Van Damme, E., & Noë, R. (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences USA*, *106*, 12007-12012.

Getty, T. (1987). Dear enemies and the prisoner's dilemma: Why should territorial neighbors form defensive coalitions? *American Zoologist*, *27*, 327-336.

Ghoul, M., Griffin, A. S., & West, S. A. (2013). Toward an evolutionary definition of cheating. *Evolution*, *68*, 318-331.

Godard, R. (1993). Tit for tat among neighboring hooded warblers. *Behavioral Ecology and Sociobiology*, *33*, 45-50.

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 699-706.

Gomes, C. M., & Boesch, C. (2011). Reciprocity and trades in wild West African chimpanzees. *Behavioral Ecology and Sociobiology*, *65*, 2183-2196.

Goto, R., Okamoto, T., Toby Kiers, E., Kawakita, A., & Kato, M. (2010). Selective flower abortion maintains moth cooperation in a newly discovered pollination mutualism. *Ecology Letters*, *13*, 321-329.

Green, W. C., Griswold, J. G., & Rothstein, A. (1989). Post-weaning associations among bison mothers and daughters. *Animal Behaviour*, *38*, 847-858.

Griffin, A. & West, S. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science, 302*, 634.

Grömping, U. (2006). Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, *17*, 1-27.

Grutter, A. S. (1999). Cleaner fish really do clean. *Nature*, *398*, 672-673.

Grutter, A. S., & Bshary, R. (2003). Cleaner wrasse prefer client mucus: support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, S242-S244.

Gubry-Rangin, C., Garcia, M., & Béna, G. (2010). Partner choice in *Medicago truncatula–Sinorhizobium* symbiosis. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1947-1951.

Haley, K. J., & Fessler, D. M. (2005). Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior*, *26*, 245-256.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I and II. *Journal of Theoretical Biology*, *7*, 1-52.

Hammer, E. C., Pallon, J., Wallander, H., & Olsson, P. A. (2011). Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability. *FEMS Microbiology Ecology*, *76*, 236-244.

Hammerstein, P. (2003). Why is reciprocity so rare in social animals? A protestant appeal. In P. Hammerstein (Ed.) *Genetic and Cultural Evolution of Cooperation* (p. 83–93). Cambridge, MA: MIT Press.

Hauser, M., McAuliffe, K., & Blake, P. R. (2009). Evolving the ingredients for reciprocity and spite. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 3255-3266.

Heil, M. (2013). Let the best one stay: Screening of ant defenders by Acacia host plants functions independently of partner choice or host sanctions. *Journal of Ecology*, *101*, 684-688.

Heil, M., Barajas-Barron, A., Orona-Tamayo, D., Wielsch, N., & Svatos, A. (2013). Partner manipulation stabilises a horizontally transmitted mutualism. *Ecology Letters*, 17, 185-192. doi: 10.1111/ele.12215.

Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science*, *269*, 1260-1262.

Hemelrijk CK (1990) Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour 39*, 1013-1029.

Hoenig, J. M., & Heisey, D. M. (2001). The abuse of power. *The American Statistician*, *55*, 19-24.

Hyman, J. (2002). Conditional strategies in territorial defense: Do Carolina wrens play tit-for-tat? *Behavioral Ecology*, *13*, 664-669.

Imhof, L. A., Fudenberg, D., & Nowak, M. A. (2005). Evolutionary cycles of cooperation and defection. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 10797-10800.

Jaeggi, A. V., De Groot, E., Stevens, J. M., & Van Schaik, C. P. (2012). Mechanisms of reciprocity in primates: Testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, *34*, 69-77.

Jaeggi, A. V., & Gurven, M. (2013). Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: A phylogenetic meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131615.

Jandér, K. C., & Herre, E. A. (2010). Host sanctions and pollinator cheating in the fig tree–fig wasp mutualism. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1481-1488.

Johnstone, R. A., Manica, A., Fayet, A. L., Stoddard, M. C., Rodriguez-Gironés, M. A., & Hinde, C. A. (2014). Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology*, *25*, 216-222.

Kalinowski, S. T. & Taper, M. L. (2006). Maximum likelihood estimation of the frequency of null alleles at microsatellite loci. *Conservation Genetics, 7,* 991–995. doi:10.1007/0592-006-9134-9.

Kalinowski, S. T., Wagner, A. P., Taper, M. L. (2006). ML‐RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes, 6,* 576-579.

Kaminski, G., Brandt, S., Baubet, E., & Baudoin, C. (2005). Life-history patterns in female wild boars (*Sus scrofa*): mother-daughter postweaning associations. *Canadian Journal of Zoology*, *83*, 474-480.

Kerth, G., Almasi, B., Ribi, N., Thiel, D., & Lüpold, S. (2003). Social interactions among wild female Bechstein's bats (*Myotis bechsteinii*) living in a maternity colony. *Acta Ethologica*, *5*, 107-114

Kiers, E. T., Rousseau, R. A., West, S. A., & Denison, R. F. (2003). Host sanctions and the legume–rhizobium mutualism. *Nature*, *425*, 78-81.

Kiers, E. T., Rousseau, R. A., & Denison, R. F. (2006). Measured sanctions: Legume hosts detect quantitative variation in rhizobium cooperation and punish accordingly. *Evolutionary Ecology Research*, *8*, 1077-1086.

Kiers, E. T., Duhamel, M., Beesetty, Y., Mensah, J. A., Franken, O., Verbruggen, E., ...Bücking, H. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, *333*, 880-882.

Koenig, B. (1994). Fitness effects of communal rearing in house mice: The role of relatedness versus familiarity. *Animal Behaviour, 48*, 1449-1457.

Koenig, B. (2006). Non-offspring nursing in mammals: General implications from a case study on house mice. In P. M. Kappeler, & C. P. van Shaik (Eds.) *Cooperation in Primates and Humans* (p. 191-205). Germany: Springer Berlin Heidelberg.

Koenig, W. D. (1988). Reciprocal altruism in birds: A critical review. *Ethology and Sociobiology*, *9*, 73-84.

Krama, T., Vrublevska, J., Freeberg, T. M., Kullberg, C., Rantala, M. J., & Krams, I. (2012). You mob my owl, I'll mob yours: Birds play tit-for-tat game. *Scientific Reports*, *2,* 800.

Krams, I., Krama, T., Igaune, K., & Mänd, R. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, *62*, 599-605.

Krams, I., Kokko, H., Vrublevska, J., Āboliņš-Ābols, M., Krama, T., & Rantala, M. J. (2013). The excuse principle can maintain cooperation through forgivable defection in the Prisoner's Dilemma game. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131475.

Kruskal, W. (1987). Relative importance by averaging over orderings. *The American Statistician*, *41*, 6-10.

Levine, M., & Ensom, M. H. (2001). Post hoc power analysis: an idea whose time has passed?. *Pharmacotherapy*, *21*, 405-409.

Ligon, J. D. (1983). Cooperation and reciprocity in avian social systems. *American Naturalist, 121*, 366-384.

Lombardo, M. P. (1985). Mutual restraint in tree swallows: A test of the Tit for Tat model of reciprocity. *Science*, *227*, 1363-1365.

Madden, J.R., Clutton-Brock, T.H. (2011). Experimental peripheral administration of oxytocin elevates a suite of cooperative behaviors in a wild social mammal. *Proceedings of the National Academy Sciences USA*, *278*, 1189–1194.

Manly, B.F.J. (2007). *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Boca Raton, FL: CRC Press.

Magphail, E. M., & Bolhuis, J. J. (2001). The evolution of intelligence: Adaptive specializations versus general process. *Biological Reviews*, *76*, 341-364.

Marshall, J. A. (2011). Group selection and kin selection: Formally equivalent approaches. *Trends in Ecology & Evolution*, *26*, 325-332.

Massen, J. J., Sterck, E. H., & de Vos, H. (2010). Close social associations in animals and humans: Functions and mechanisms of friendship. *Behaviour*, *147*, 1379-1412.

Masters, W. M., & Waite, T. A. (1990). Tit-for-tat during predator inspection, or shoaling? *Animal Behaviour*, *39*, 603-604.

McNab, B. K. (1973). Energetics and the distribution of vampires. *Journal of Mammalogy*, 131-144.

McCulloch, E. V. E., & Stevens, R. D. (2011). Rapid development and screening of microsatellite loci for *Artibeus lituratus* and their utility for six related species within Phyllostomidae. *Molecular Ecology Resources*, *11*, 903-913.

Melis, A. P., Hare, B., & Tomasello, M. (2008). Do chimpanzees reciprocate received favours? *Animal Behaviour*, *76*, 951-962.

Milinski, M. (1987). Tit for tat in sticklebacks and the evolution of cooperation. *Nature*, *325*, 433-435.

Milinski, M., David, K., & Kettler, R. (1990). Tit for tat: Sticklebacks (*Gasterosteus aculeatus*) 'trusting' a cooperating partner. *Behavioral Ecology*, *1*, 7-11.

Milinski, M., Lüthi, J. H., Eggler, R., & Parker, G. A. (1997). Cooperation under predation risk: Experiments on costs and benefits. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*, 831-837.

Mooney, S. J., Douglas, N. R., & Holmes, M. M. (2014). Peripheral administration of oxytocin increases social affiliation in the naked mole-rat *Heterocephalus glaber*. *Hormones and Behavior*, *65,* 380-385.

Moses, R. A., & Millar, J. S. (1994). Philopatry and mother-daughter associations in bushy-tailed woodrats: space use and reproductive success. *Behavioral Ecology and Sociobiology*, *35*, 131-140.

Neumann I. D., Maloumby R., Beiderbeck D. I., Lukas M., Landgraf R. (2013). Increased brain and plasma oxytocin after nasal and peripheral administration in rats and mice. *Psychoneuroendocrinology, 38,* 1985–1993. doi: 10.1016/j.psyneuen.2013.03.003.

Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour*, *71*, 1-18.

Noë, R., & Hammerstein, P. (1994). Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, *35*, 1-11.

Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution*, *10*, 336-339.

Noë, R., & Hammerstein, P. (2001). *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*. UK: Cambridge University Press.

Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, *314*, 1560-1563.

Olendorf, R., Getty, T., & Scribner, K. (2004). Cooperative nest defence in red–winged blackbirds: Reciprocal altruism, kinship or by–product mutualism? *Proceedings of the Royal Society B: Biological Sciences*, *271*, 177-182.

Orona-Tamayo, D., & Heil, M. (2013). Stabilizing mutualisms threatened by exploiters: New insights from ant–plant research. *Biotropica*, *45*, 654-665.

Orona-Tamayo, D., Wielsch, N., Blanco-Labra, A., Svatos, A., Farías-Rodríguez, R., & Heil, M. (2013). Exclusive rewards in mutualisms: Ant proteases and plant protease inhibitors create a lock–key system to protect Acacia food bodies from exploitation. *Molecular Ecology*. *22*, 4087-100. doi: 10.1111/mec.12320.

Paolucci, M., Conte, R., & Di Tosto, G. (2006). A model of social organization and the evolution of food sharing in vampire bats. *Adaptive Behavior*, *14*, 223-238.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M., & Bonhoeffer, S. (2005). Evolution of cooperation by generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 1115-1120.

Piaggio, A., Johnston, J. & Perkins, S. (2008). Development of polymorphic microsatellite loci for the common vampire bat, *Desmodus rotundus* (Chiroptera, Phyllostomidae). *Molecular Ecology Resources, 8*, 440-442.

Pinker, S., Nowak, M. A., & Lee, J. J. (2008). The logic of indirect speech. *Proceedings of the National Academy of Sciences USA*, *105*, 833-838.

Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, *21*, 1140-1144.

Pitcher, T. J., Green, D. A., & Magurran, A. E. (1986). Dicing with death: Predator inspection behaviour in minnow shoals. *Journal of Fish Biology*, *28*, 439-448.

Pusey, A. E., & Packer, C. (1997). The ecology of relationships. In J. R. Krebs, & N. B. Davies (Eds.) *Behavioural Ecology: An Evolutionary Approach,* 4th ed (p. 254-283).

Rand, D. G., Greene, J. D., & Nowak, M. A. (2012). Spontaneous giving and calculated greed. *Nature*, *489*, 427-430.

Raihani, N. J., Grutter, A. S., & Bshary, R. (2010). Punishers benefit from third-party punishment in fish. *Science*, *327*, 171-171.

Raihani, N. J., & Bshary, R. (2011). Resolving the iterated prisoner's dilemma: theory and reality. *Journal of Evolutionary Biology*, *24*, 1628-1639.

Raihani, N. J., Pinto, A. I., Grutter, A. S., Wismer, S., & Bshary, R. (2012). Male cleaner wrasses adjust punishment of female partners according to the stakes. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 365-370.

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C., & Thierry, B. (2006). Accepting loss: The temporal limits of reciprocity in brown capuchin monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 179-184.

Ratnieks, F. L., & Wenseleers, T. (2008). Altruism in insect societies and beyond: voluntary or enforced?. *Trends in Ecology & Evolution*, *23*, 45-52.

Ratnieks, F. L., Foster, K. R., & Wenseleers, T. (2011). Darwin's special difficulty: the evolution of "neuter insects" and current theory. *Behavioral Ecology and Sociobiology*, *65*, 481-492.

Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S., & Kilts, C. D. (2002). A neural basis for social cooperation. *Neuron*, *35*, 395-405.

Romero, T., Nagasawa, M., Mogi, K., Hasegawa, T., Kikusui, T. (2014). Oxytocin promotes social bonding in dogs. *Proceedings of the National Academy of Sciences USA*, *111*, 9085-9090.

Russell, A. F., & Wright, J. (2009). Avian mobbing: Byproduct mutualism not reciprocal altruism. *Trends in Ecology & Evolution*, *24*, 3-5.

Rutte, C., & Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): Direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology*, *62*, 499-505.

Sabbatini, G., Vizioli, A. D. B., Visalberghi, E., & Schino, G. (2012). Food transfers in capuchin monkeys: An experiment on partner choice. *Biology Letters*, *8*, 757-759.

Salwiczek, L. H., & Bshary, R. (2011). Cleaner wrasses keep track of the 'when' and 'what' in a foraging task. *Ethology*, *117*, 939-948.

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., ...Bshary, R. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orangutans in a complex foraging task derived from cleaner–client reef fish cooperation. *PLOS One*, *7*, e49068.

SAS Institute Inc. 2013. JMP® 11. Cary, NC: SAS Institute Inc.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, *20*, 2207-2210.

Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: A meta-analysis. *Biology Letters*, *4*, 9-11.

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior*, *39*, 45-69.

Schino, G., & Aureli, F. (2010a). A few misunderstandings about reciprocal altruism. *Communicative & Integrative Biology*, *3*, 561-563.

Schino, G., & Aureli, F. (2010b). Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*, 130-135.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, *20*, 2207-2210.

Shultz, S., & Dunbar, R. I. (2007). The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 2429-2436.

Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, *308*, 541-543.

Seyfarth, R. M., & Cheney, D. L. (1988). Empirical tests of reciprocity theory: problems in assessment. *Ethology and Sociobiology*, *9*, 181-187.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*, 153-177.

Sella, G. (1985). Reciprocal egg trading and brood care in a hermaphroditic polychaete worm. *Animal Behaviour*, *33*, 938-944.

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, *61*, 183-195.

Shackelford, T. K., & Buss, D. M. (1996). Betrayal in mateships, friendships, and coalitions. *Personality and Social Psychology Bulletin*, *22*, 1151-1164.

Silk, J. B. (2003). Cooperation without counting. In P. Hammerstein (Ed.) *Genetic and cultural evolution of cooperation* (p. 37-54). Cambridge, MA: MIT Press.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., …Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*, 1359-1361.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, relationship quality, and solicitation pressure on food transfers. *Animal Behavior*, *85*, 941-947.

Simpson, E. A., Sclafani, V., Paukner, A., Hamel, A. F., Novak, M. A., Meyer, J. S., Suomi, S. J., Ferrari, P. F. (2014). Inhaled oxytocin increases positive social behaviors in newborn macaques. *Proceedings of the National Academy of Sciences USA, 111,* 6922-6927.

Smith, A.S., Ågmo, A., Birnie, A.K., French, J.A. (2010). Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. *Hormones and Behavior,* 57, 255–262.

Stephens, D. W., Anderson, J. P., & Benson, K. E. (1997). On the spurious occurrence of Tit for Tat in pairs of predator-approaching fish. *Animal Behaviour*, *53*, 113-131.

Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an iterated prisoner's dilemma. *Science*, *298*, 2216-2218.

Stevens, J. R., & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, *8*, 60-65.

Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, *36*, 499-518.

Taborsky, M. (2013). Social evolution: reciprocity there is. *Current Biology*, *23*, R486-R488.

Taylor, C. E., & McGuire, M. T. (1988). Reciprocal altruism: 15 years later. *Ethology and Sociobiology*, *9*, 67-72.

Tooby, J., & Cosmides, L. (1996). Friendship and the banker's paradox: Other pathways to the evolution of adaptations for altruism. *Proceedings of the British Academy*, *88*, 119-143.

Tooby, J., & Cosmides, L. (2008). The evolutionary psychology of the emotions and their relationship to internal regulatory variables. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *Handbook of Emotions,* 3rd ed. (p. 114-137.) New York: Guilford.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35-57.

Trivers, R. (2006). Reciprocal altruism: 30 years later. In *Cooperation in Primates and Humans* (p. 67-83). Germany: Springer Berlin Heidelberg.

Tschapka, M., Wilkinson, G.S. (1999). Free-ranging vampire bats (*Desmodus rotundus*, Phyllostomidae) survive 15 years in the wild. *Zeitschrift für Säugetierkunde, 64*, 239-240.

Van Cleve, J., & Akcay, E. (2014). Pathways to social evolution: reciprocity, relatedness, and synergy. *Evolution*, *68*, 2245-2258.

Veening J. G., Olivier B. (2013). Intranasal administration of oxytocin: behavioral and clinical effects, a review. *Neuroscience & Biobehavioral Reviews, 37*, 1445–1465 10.1016/j.neubiorev.2013.04.012.

Voigt, C. C., Voigt‐Heucke, S. L., & Schneeberger, K. (2012). Isotopic data do not support food sharing within large networks of female vampire bats (*Desmodus rotundus*). *Ethology*, *118*, 260-268.

Waltz, E. C. (1981). Reciprocal altruism and spite in gulls: A comment. *The American Naturalist*, *118*, 588-592.

Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: Fitness consequences of social partner choice in female house mice. *Animal Behaviour*, *75*, 801-808.

Weidt, A., Lindholm, A. K., & König, B. (2014). Communal nursing in wild house mice is not a by-product of group living: Females choose. *Naturwissenschaften*, *101*, 73-76.

West, S. A., Kiers, E. T., Simms, E. L., & Denison, R. F. (2002). Sanctions and mutualism stability: Why do rhizobia fix nitrogen? *Proceedings of the Royal Society B: Biological Sciences*, *269*, 685-694.

West, S. A., Griffin, A. S., & Gardner, A. (2007a). Evolutionary explanations for cooperation. *Current Biology*, *17*, R661-R672.

West, S. A., Griffin, A. S., & Gardner, A. (2007b). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, *20*, 415-432.

West, S. A., El Mouden, C., & Gardner, A. (2011). Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior*, *32*, 231-262.

West-Eberhard, M. J. (1975). The evolution of social behavior by kin selection. *Quarterly Review of Biology*, *50*, 1-33.

Wheatcroft, D. J., & Krams, I. (2009). Response to Russell and Wright: Avian mobbing. *Trends in Ecology & Evolution*, *24*, 5-6.

Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, *308*, 181-184.

Wilkinson, G. S. (1985). The social organization of the common vampire bat. I and II. *Behavioral Ecology and Sociobiology, 17*, 111-134.

Wilkinson, G. S. (1986). Social grooming in the common vampire bat, *Desmodus rotundus*. *Animal Behavior, 34*, 1880-1889.

Wilkinson, G. S. (1988). Reciprocal altruism in bats and other mammals. *Ethology and Sociobiology*, *9*, 85-100.

Witkowski, M. (2007). Energy sharing for swarms modeled on the common vampire bat. *Adaptive Behavior*, *15*, 307-328.

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 281*, 1778, 20133096.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765-778.

Xue, M., & Silk, J. B. (2012). The role of tracking and tolerance in relationship among friends. *Evolution and Human Behavior*, *33*, 17-25.

Zöttl, M., Heg, D., Chervet, N., & Taborsky, M. (2013). Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. *Nature Communications*, *4*, 1341.