



Original Article

Food-sharing vampire bats are more nepotistic under conditions of perceived risk

Gerald G. Carter^a, Gerald S. Wilkinson^b and Rachel A. Page^a

^aSmithsonian Tropical Research Institute, Luis Clement Ave., Tupper Building 401, Balboa, Ancón, Panamá, República de Panamá and ^bDepartment of Biology, University of Maryland, 4094 Campus Drive, College Park, MD, USA

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Cooperative behaviors exist along a spectrum of cost, from no-risk scenarios of mutual benefit to self-sacrificing altruism. Hamilton's rule predicts that as risk increases, cooperative decisions should become increasingly kin-biased (nepotistic). To manipulate the perceived risks of regurgitated food sharing in captive vampire bats, we created a novel "rescue" condition, which required that donors leave their preferred roosting location, descend to an illuminated spot on the cage floor, and regurgitate food across cage bars to a trapped hungry bat. Vampire bats adapted their food sharing to this novel context, but with a dramatic reduction in the probability and amount of food sharing. Sixteen of 29 bats were fed by groupmates when trapped. All 15 starved bats that were tested in both trapped and free conditions received less food when trapped. Donations to trapped bats came from kin and nonkin, but subjects received a greater proportion of their food from closer relatives when trapped than when free. This finding supports the prediction that nepotistic biases should be exaggerated under dangerous conditions.

Key words: cooperation, food sharing, kin selection, nepotism, rescue behavior, vampire bats.

INTRODUCTION

Hamilton's Rule ($rB > C$) states that helping is adaptive when the benefit to the recipient (B), scaled by the recipient's relatedness (r) exceeds the cost to the helper (C) (Hamilton 1964; West et al. 2001). Behavioral ecologists typically categorize cooperation based on whether helping poses a net direct fitness cost (altruism) or benefit (mutual benefit), but this binary classification is not always useful (West et al. 2007a, 2007b). Many cooperative traits increase direct and indirect fitness, and can be conceptualized as falling along a spectrum of the reliability of direct fitness benefits, from mutual benefit that is always positive and zero risk on one end, to altruism where direct fitness is always negative on the other. Between these endpoints are situations where evolutionary stability of helping requires indirect fitness or enforcement because the net direct fitness benefits are unreliable. As the reliability of net direct fitness benefits decreases (i.e. greater risk), indirect fitness becomes more necessary for stabilizing cooperation.

Accordingly, we should expect a positive relationship between the perceived risk of helping and the importance of kinship in helping decisions. This correlation should be evident in "rescue behavior" defined as targeted helping of a distressed victim that does not immediately benefit the rescuer but rather places it at risk of

injury or mortality (Nowbahari et al. 2009; Nowbahari and Hollis 2010). To understand how animals make cooperative decisions, experiments on rescue behavior can test the roles of perceived risk, kinship, and victim need (Nowbahari and Hollis 2010; Hollis and Nowbahari 2013b; Miler 2016; Nowbahari et al. 2016). Rescuers should tolerate greater risks to help closer kin and be more discriminating in whom they rescue in more risky conditions. For example, parents are expected to put themselves at greater risk when defending or rescuing their offspring from predators compared to when cooperatively mobbing the same predators with nonkin.

Common vampire bats (*Desmodus rotundus*) regurgitate blood for unfed kin and nonkin of high association (Wilkinson 1984). Evidence suggests that bats donate food to cement bonds that promote reciprocal sharing and to increase survival of close kin (Carter and Wilkinson 2013a, 2013b, 2015; Wilkinson 1984, 1988). As predicted by Hamilton's rule, food sharing in vampire bats is positively predicted by kinship, the recipient's benefit, and the donor's cost, where costs and benefits are the estimated effects on starvation risk (Wilkinson 1984). Food donations to nonkin appear to help create and maintain bonds leading to reciprocal help at a relatively small starvation risk (Wilkinson 1984; Carter and Wilkinson 2015).

Sharing decisions might also depend on other risks. If food sharing was more energetically difficult or posed a greater risk of injury or predation, then helping decisions should become more nepotistic, such that recipients would receive a higher proportion of their food from closer kin relative to distant kin or nonkin. To

Address correspondence to G. Carter. E-mail: gerry@socialbat.org.

manipulate donor risk, we trapped a starved vampire bat inside a small cage on the ground in the corner of a larger home cage. We chose the least-visited corner that was most distant to the bats' preferred roosting spot and brightest, because vampire bats are highly averse to light (e.g. Crespo et al. 1972). The trapped condition required that a donor pass food across cage bars after descending to the ground. Although vampire bats are adept on the ground (Riskin et al. 2006), they are vulnerable to ground predators (e.g. Delpietro et al. 1994, Martin-Solano et al. 2016), and even captive-born bats are far more vigilant and prone to flight on the ground than when hanging (Carter, personal observation). By comparing donations to trapped bats on the ground and to the same bats under more natural freely moving conditions, we asked 2 questions. Can vampire bats adapt food sharing to this novel risky context? If so, is sharing in this rescue context more nepotistic?

METHODS

Subjects

We conducted tests in a captive colony of 14 female and 28 male vampire bats from 5 matrilineal groups sourced from 3 zoos, cared for by the Organization of Bat Conservation at the Cranbrook Institute of Science (Bloomfield Hills, MI, USA, see (Carter and Wilkinson 2016) for husbandry details). Procedures were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-10-63).

Bats were individually marked with passive integrated transponder (PIT) tags. All bats older than 2 years were also marked with unique forearm bands; younger bats were identified using distinctive face or body markings or by scanning their PIT tag during observation. To estimate pairwise relatedness, we calculated the dyadic maximum likelihood estimator in the 'related' R package (Wang 2011; Pew et al. 2015) using genotypes from 19 polymorphic microsatellites (Carter and Wilkinson 2015). To avoid potential biases caused by estimating background allele frequencies from this captive population, we used a maternal pedigree to adjust the values for all known relationships (0.5 for parent-offspring, 0.25 for grandparent, etc).

Food-sharing experiment

During each of 37 trials, we isolated and fasted a subject overnight for at least 24 h. Food sharing trials were conducted inside a $3 \times 1.5 \times 2$ m home flight cage and began between 1725 and 2115 h. During the trapped condition, the food-deprived subject was constrained in a $0.1 \times 0.2 \times 0.2$ m wire cage on the floor for 1 h. As explained above, the trapped condition should be perceived by potential food donors as more risky because donors must descend to an illuminated location they usually avoid. We tested 29 different bats (13 females and 16 males) in the trapped condition (37 trials) and weighed each subject before and after. We accounted for repeated measures of the 8 bats tested twice (see statistical analyses described below). On 22 of the 37 trials, we released the subject bat ($N = 15$) after the trapped condition directly into the home flight cage unrestrained for 2 h (free condition). We then weighed it again afterwards. During both conditions, we used a Sony Nightshot camcorder and infrared spotlight to record the subject bat and its interactions with cagemates. Following past work (Carter and Wilkinson 2013b), we measured amounts of food sharing by scoring the partner identity and duration of events where the subject licked the mouth of another bat for at least 5 s. To confirm

sharing across cage bars, we used linear regression to test the effect of mouth-licking time on weight change during the trapped condition, after natural log-transforming both variables. To calculate the 95% confidence intervals of food received by bats in each trial hour, we used the BCa method of bootstrapping (Puth et al. 2015).

Is rescue behavior more nepotistic?

To test whether food sharing in the trapped condition was more nepotistic than normal sharing, we used 2 alternative approaches for testing the null hypothesis. First, for each bat's trapped and free periods, we calculated paired "nepotism scores" that were the sum of all contributions to a subject's total food received in a trial with each contribution scaled by the donor's relatedness:

$$\sum_t \frac{d_i r_i}{t}$$

where d is food from donor i (seconds the subject licked the mouth of bat i), r is the subject's pairwise kinship with donor i and t is the subject's total mouth-licking time with all donors in the trial. We calculated a mean nepotism score for any subjects tested twice. We used a paired t -test to compare the nepotism score in the trapped condition versus the normal condition for the 7 bats fed in both conditions.

For the second approach, we measured nepotism as a positive interaction between kinship and the trapped condition as factors driving a donor's relative contribution to a subject. Specifically, we predicted that the effect of kinship would be larger during the trapped condition compared to the free condition. We used a randomization test applied to a general linear mixed model (lmer in R) where we predicted the logit-transformed proportion of total food received by a subject from a donor based on treatment (whether the subject was trapped or free), donor kinship, and the interaction between these 2 fixed effects, while controlling for dyad, and trial nested within dyad, as random effects to account for repeated measures. Proportion of total food received is an appropriate response variable to measure because nepotism is higher either when kin contribute relatively more or when nonkin contribute relatively less. We used logit-transformation of proportions to increase normality after subtracting the rounded minimum value from the response variable (Warton and Hui 2011). To calculate p -values, we compared the observed fixed effects to a distribution of 5000 null fixed effects where treatment and kinship were randomized, as expected under the null hypothesis.

RESULTS

We recorded 519 regurgitation events, which we summed into 106 dyadic trial donations using all events where we could positively identify the donor (94.4% of total food sharing duration). Nine of 16 males and 7 of 13 females were fed by cagemates across cage bars (video: Carter 2016). Mouth-licking times explained 93% of the variation in weight change during the time the subject was trapped in the cage (both measures natural-log-transformed; $F(1,9) = 113.8$, $P < 0.0001$). Donors to trapped bats included 6 mothers, 2 daughters, 1 son, 4 half-siblings, 1 cousin, and 6 distant kin or nonkin.

All 15 of the bats tested in both the trapped and free condition received more food after being released from the cage. Food received by these subjects (mean and 95% CI of mouth-licking time) increased from 6 s (2–22 s) during the trapped condition to 772 s (525–925 s) during the first hour after the bats were freed,

and then decreased again to 101 s (33–249 s) in the next hour (Figure 1a). Only 7 of these 15 bats were fed when trapped, and these donation sizes were on average only 28% of what they were fed when freed.

The nepotism score was always higher during the trapped condition (paired $t = 3.7$, $df = 6$, $P = 0.01$, Figure 1b). For predicting the relative contribution of a donor to a subject's total food received, there was a positive interaction between kinship and the trapped condition ($P = 0.0086$). Closer relatives contributed a greater proportion of the subjects' food received during the trapped condition.

DISCUSSION

We show that vampire bats can adapt food sharing to a novel context, regurgitating food across cage bars for both hungry kin and nonkin. This flexible targeted helping fits the definition of rescue behavior (Nowbahari et al. 2009; Nowbahari and Hollis 2010), which has also been described in striped dolphins (Siebenaler and Caldwell 1956), capuchin monkeys (Vogel and Fuentes-Jiménez 2006), rats (Ben-Ami Bartal et al. 2011; Vasconcelos et al. 2012; Silberberg et al. 2014), and several ant species (Czechowski et al. 2002; Nowbahari et al. 2009; Hollis and Nowbahari 2013a; Taylor et al. 2013). Donors were likely attracted by some combination of a trapped bat's echolocation and contact calls (Carter and Wilkinson 2016), because they selectively flew down to visit the trapped bats that they fed; they did not visit every bat to decide whether to feed them.

When bats were trapped, they were half as likely to receive food, and when they were fed they received far less. The difference in total food received between trapped and free conditions cannot be easily explained by time-of-day effects (e.g. sharing rates peaking at a certain hour every day) because trial start times varied by several hours, or by the order of experimental conditions (e.g. sharing rates increasing with time) because total food received always increased when the bat was freed and then declined in the second hour of the free condition (Figure 1a). The dramatic decline of food sharing in

the rescue condition is likely to result from 3 nonmutually exclusive factors: novelty, difficulty, and perceived risk.

Novel or artificial scenarios often fail to trigger the evolved cognitive mechanisms that underlie cooperation. Human prosociality, e.g. is often triggered more by social cues than by economic costs and benefits. Likewise, given that human social cognition evolved under conditions of repeated interactions with real people, it is not surprising that human subjects make maladaptive decisions in the artificial context of “one-shot” economic games on computers (Delton et al. 2011; Burton-Chellew and West 2013). Similarly, animal subjects in cooperation experiments are less likely to help each other when they cannot choose their partner, when contact between partners is limited, or when there are other artificial constraints (Silk et al. 2005; Noë 2006; Horner et al. 2011; Jaeggi et al. 2013; Carter 2014). Nonhuman primates are more likely to demonstrate evidence of reciprocal cooperation in naturalistic group settings than in studies with instrumental tasks and explicit turn-taking (Jaeggi et al. 2013). Capuchin monkeys can coordinate with a partner to simultaneously pull a tray of food, but have far less success in a more artificial version of the same task which requires simultaneously pressing levers to obtain juice from an electronic device (Mendres and de Waal 2000). After a successful hunt in the wild, chimpanzee males might share meat with male hunting partners (Mitani and Watts 2001) or females (Gomes and Boesch 2009), but chimpanzees might not share food across cage bars or pull a lever to deliver food to that same partner in a nearby cage (Silk et al. 2005; Noë 2006; Horner et al. 2011; Jaeggi et al. 2013).

Vampire bats might therefore not have shared food across cage bars if this context was too unnatural. Normal regurgitated food sharing is fairly stereotyped. It can be initiated by either donors or recipients: one bat approaches the other, the bats then sniff and groom each other, often belly-to-belly, then either the recipient begins licking the donor's lips or the donor may first lick the recipient's face, which triggers the recipient to lick the donor's lips. The donor responds by either turning away to reject the begging bat or holding still while the unfed bat rapidly licks the donor's slightly open mouth (Carter 2016). In the trapped condition, several of these behaviors were restricted, including social grooming, close physical contact, and approach by the hungry potential recipient. The results here show that this series of typical behaviors is not required for bats to share and further support past findings that nonkin sharing is not driven by harassment (Carter and Wilkinson 2013b). However, restrictions on physical contact, begging, and social grooming may have played a large role in reducing food sharing. In particular, social grooming appears to promote food sharing because it is far more frequent in vampires than in other social bats that do not share food (Wilkinson 1986; Carter and Wilkinson 2013b; Carter and Leffer 2015), and it often occurs before food sharing (Wilkinson 1986).

The trapped bat condition should be perceived as more costly and risky to potential donor bats for several reasons. The location where the cage was placed was the brightest, the most distant to where the bats roost, and the least-visited spot in the cage based on >200 h of observation. We had never previously seen food sharing occur on the ground. Captive bats appear to perceive the ground as less safe because slight disturbances cause grounded bats to take flight and retreat to the ceiling. If food sharing in the rescue condition was simply more cognitively difficult, but not perceived by the bats as more costly or risky, then the propensity to share food should decline, but the degree of nepotism should remain the same.

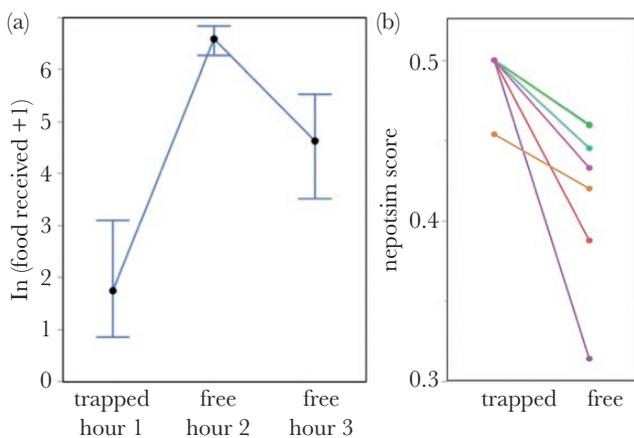


Figure 1

Effects of trapped condition on food sharing. (a) Bats received less food when trapped than when free. Plot shows means and bootstrapped 95% confidence intervals for natural-log-transformed food received (seconds of mouth licking + 1) in each hour of the experiment. (b) Food sharing is more nepotistic when bats are trapped. Change in nepotism scores are shown for the 7 bats fed in both the trapped and free conditions. The highest line overlaps another one that connects similar values.

This is not what we found; a higher proportion of food donations came from closer kin in the trapped condition.

Food donations involve a relatively small portion of a bat's ingested meal and pose a relatively small risk to donor survival compared to the indirect fitness benefit of saving a close relative's life or the direct benefit of promoting future reciprocal help (Wilkinson 1984, 1988). Females make larger food donations to their offspring and mothers, suggesting that closer kin are more willing to incur greater energetic risks (Carter and Wilkinson 2013b, 2015). Our results here suggest that closer kin donors are also more willing to endure greater situational risk.

In the greater spear-nosed bat (*Phyllostomus hastatus*), maternal and nonkin helpers appear to help at different levels of cost to themselves (Bohn et al. 2009). Greater spear-nosed bat pups that fall to the cave floor are often attacked by females from other groups. Unrelated females from the same group will fly down and guard the pup from these attackers, but only the pup's mother will actually retrieve it (Bohn et al. 2009). This may be because females in the group are typically lactating at the same time (Porter and Wilkinson 2001) and retrieving a pup would likely allow it to latch on to a female's nipple and nurse. Such milk theft has been seen in other bats (McCracken 1984).

The results here do not demonstrate that kinship cues *per se* were more important than past social experience for driving the nepotistic patterns we observed. Indeed, the role of past social experience (reciprocal help) might also be more important for rescue behavior, but we lack the power to test this hypothesis, because we lack rates of past sharing to and from most of the male bats. Nepotism and reciprocity are not mutually exclusive hypotheses and can be reinforcing stabilizers of cooperation. Previous work has shown that reciprocal sharing was more important than kinship for predicting both food sharing rates (Carter and Wilkinson 2013b) and attraction to the playback of contact calls from a trapped, isolated conspecific (Carter and Wilkinson 2016). There is also evidence for a positive relationship between kinship and reciprocal sharing, because sharing rates in related pairs are both greater and more balanced (Carter and Wilkinson 2013b). Our findings are therefore consistent with the notion that nepotism is stronger, because bats form their strongest social bonds with maternal kin, and they are more willing to help individuals with whom they have the strongest sharing bonds. The larger point is that under increased risks, helpers should be more discriminating in their cooperative investments whether this discrimination is based on kinship or past experience (Krama et al. 2012).

This study adds to 5 decades of evidence showing that animal helping decisions are influenced by interactions between cues to recipient kinship, recipient benefit, and helper costs (e.g. Koenig and Dickinson 2016) as predicted by Hamilton's Rule. Helping decisions across various cooperative breeding species become more nepotistic when the recipients will benefit more from the help (Griffin and West 2003; Cornwallis et al. 2009). The direct fitness benefits for helpers and recipients can either correlate or conflict, depending on the environment. Cues to recipient benefit can therefore vary in reliability and importance across species. An illustrative example comes from comparisons of parental care across bird species (Caro et al. 2016). For bird species where chick siblings are in stark competition for survival, chick begging is a less honest indicator of need and parents pay less attention to it. Instead, parents use signals of chick quality to decide which offspring to invest in and which to let die. In contrast, in bird species where parents can successfully raise all their offspring, the interests of parents and chicks are aligned, begging is a better cue to need, and parents pay more attention to it (Caro et al. 2016).

Within a single species, the returns from cooperative investments can also vary by context based on the partner's propensity to reciprocate (Krams et al. 2008; Rutte and Taborsky 2008), the supply and demand of alternative partners (Fruteau et al. 2009), the energetic costs of helping (Schneeberger et al. 2012), or the perceived predation risks to the helper (Krams et al. 2010; Krama et al. 2012). In lab experiments with rats trained to pull bars to deliver food, the degree of contingent reciprocity increased with the physical difficulty of pulling (Schneeberger et al. 2012). In field experiments that induced cooperative mobbing, pairs of pied flycatchers decided whether or not to help neighboring pairs based on an interaction between the past reciprocal help received from that neighboring pair and the risk to the helper (Krams et al. 2008; Krama et al. 2012). That is, when predators threatened neighbors that were nearby (20–24 m), the subjects always helped their neighbors mob a predator regardless of past defections. But at farther distances (48–84 m), help was conditional on prior reciprocal mobbing assistance (Krama et al. 2012). This makes sense because, when a predator is nearby, mobbing is immediately and directly beneficial to all actors, and the risk does not depend on whether one helps or not. In contrast, when a predator is farther away, helping a neighbor incurs a personal risk that one could otherwise avoid. In this case, mobbing is a cooperative investment, not a byproduct of selfish behavior, and birds should use past experience to decide to help or not (Carter 2014).

Rather than classifying behaviors as either mutual benefit or kin-selected altruism, these examples show that much insight can be gained from thinking about cooperation as existing along a continuous spectrum from 100% direct fitness benefits to 100% indirect fitness benefits. In between these endpoints, we might expect that different risks favor different kinship biases. To illustrate this, consider J.B.S. Haldane's famous quip that he would risk jumping in a river to save 2 brothers or 8 cousins (Haldane 1955; Smith 1975). If helping a friend provides any direct fitness benefit, then a nepotistic Haldane might tolerate the minimal risk of wading into shallow water to help an unrelated friend.

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DATA ACCESSIBILITY

Analyses reported in this article can be reproduced using the data and R script provided by Carter et al. (2017).

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