

1 **Social bet-hedging in vampire bats**

2 Gerald G. Carter¹

3 Damien Farine^{2,3,4}

4 Gerald S. Wilkinson⁵

5

6 1. Smithsonian Tropical Research Institute, Balboa, Ancòn, Panama

7 2. Department of Collective Behaviour, Max Planck Institute for Ornithology, Konstanz,
8 Germany

9 3. Chair of Biodiversity and Collective Behaviour, Department of Biology, University
10 of Konstanz, Germany

11 4. Department of Zoology, University of Oxford, UK

12 5. University of Maryland, College Park, USA

13

14

Abstract

Helping kin or nonkin can provide direct fitness benefits, but helping kin also benefits indirect fitness. Why then should organisms invest in cooperative partnerships with nonkin, if kin relationships are available and more beneficial? One explanation is that a kin-limited support network is too small and risky. Even if additional weaker partnerships reduce immediate net cooperative returns, individuals extending cooperation to nonkin can maintain a larger social network that reduces the potential costs associated with losing a primary cooperation partner. Just as financial or evolutionary bet-hedging strategies can reduce risk, investing in *quantity* of social relationships at the expense of relationship *quality* (“social bet-hedging”) can reduce the risks posed by unpredictable social environments. Here, we provide evidence for social bet-hedging in food-sharing vampire bats. When we experimentally removed a key food-sharing partner, females that previously fed a greater number of unrelated females suffered a smaller reduction in food received. Females that invested in more nonkin bonds did not do better under normal conditions, but they coped better with partner loss. Hence, simulating loss of a key partner revealed the importance of weaker nonkin bonds. Social bet-hedging can have important implications for social network structure by influencing how individuals form relationships.

Keywords:

biological markets, centrality, cooperation, bet-hedging, reciprocity, social networks

37

38 **Introduction**

39 When cooperative relationships require an investment of time or energy,
40 individuals should invest preferentially in the partner yielding the greatest cooperative
41 returns [1-3]. However, if cooperative relationships take time to develop and partners are
42 not always available, then a strategy that focuses investments in the single most-
43 profitable partnership is risky. When partner availability is unpredictable, a better
44 strategy would diversify cooperative investments across more partners to reduce the
45 potential costs of losing a key partnership. We call this strategy *social bet-hedging*. Like
46 other forms of bet-hedging [4], this strategy can be advantageous even if it reduces
47 average short-term returns.

48 Bet-hedging strategies avoid risk. Social bet-hedging is analogous to evolutionary
49 bet-hedging, where phenotypes with less temporally variable reproductive success
50 outbreed phenotypes yielding reproductive success that is higher on average but more
51 temporally variable [4]. This occurs because optimizing growth rates (or returns on
52 investment) requires increasing the geometric, rather than arithmetic, mean. An
53 evolutionary bet-hedging strategy can maximize geometric mean fitness, even at the
54 expense of a lower arithmetic mean fitness, by coping better with rare stressful conditions
55 [4].

56 By spreading cooperative investments to more partners, social bet-hedging
57 strategies can reduce the temporal variance in cooperative returns caused by changes in
58 partner availability. Investing in new relationships can be beneficial even if this requires
59 diverting time and energy away from the most-profitable cooperative relationship that

yields the greatest inclusive fitness return rate (e.g. the strongest reciprocator or closest kin).

Social bet-hedging might explain why female common vampire bats (*Desmodus rotundus*) that have strong reciprocal food-sharing relationships with close kin still regurgitate food to other nonkin [5-7]. Vampire bats are susceptible to starvation and depend on a network of food-sharing partners to feed them after unsuccessful foraging nights. The strongest, most reliable, and most balanced food-sharing bonds develop between mothers and daughters, but even for these close kin, the direct fitness benefits of food sharing might exceed the indirect fitness benefits [5-10]. The best known predictor of sharing rates within familiar pairs is not kinship, but the reciprocal rate of sharing [5, 8]. If feeding close kin yields reciprocal sharing benefits that are equal or greater to feeding nonkin, why invest in nonkin bonds?

Sharing only with kin could be risky because relatives can be lost for various reasons. A starved female with only one or a few close maternal kin in her food-sharing network might not find her primary close kin donor, for example, if this partner also failed to feed or switched to a different roost on that night—which happens frequently [10]. To compensate for this risk, a social bet-hedging female would foster new bonds by diverting some of her social time and energy away from mothers and daughters and towards other females. Even if each of these additional partners is less related and reciprocates less, this strategy could dramatically increase long-term survival by reducing the risk of failing to find a primary donor when in dire need.

To test this idea, we quantify the impact, in terms of total food received, of removing a past key food donor for individual bats in need. Previously, Carter &

Wilkinson [6] demonstrated that females that fed more nonkin females in previous years subsequently received more food in the absence of this key donor (see methods), but this finding could simply mean that better-connected bats always receive more food. Here, we extend our analysis of this experiment to show that, as predicted by social bet-hedging, helping more nonkin did not increase food received when key donors were available, but it reduced the negative impact on food received when a key donor was removed.

Methods

We used data from a previous experiment [6], where a female subject was isolated and fasted for 24 hours, then reintroduced to a captive colony of 27-34 individually-marked conspecifics to measure food donated by each groupmate. Mean dyadic donation rates were calculated from 1337 dyadic regurgitation observations among 14 captive females using 91 fasting trials over a 4-year period [see supplement, 6]. Relatedness was estimated using maternal pedigree and 19 microsatellite markers [see 6]. For each female, a unique *key donor* with a strong history of food sharing was selected for temporary removal; key donors were either the subject's highest-ranking donor (9 cases), second-highest ranking donor (4 cases), or a lower-ranking donor and the highest-ranking recipient (1 case) [see supplement, 6]. During two control trials, a female that had never fed the subject was excluded by either removing it or fasting it on the same night. During three subsequent test trials, the subject's key donor was similarly excluded [6]. A previous analysis showed that bats that fed more nonkin females in past years received more food during test trials [6], but the social bet-hedging hypothesis predicts that this relationship should only exist when key donors are removed, not when they are present.

Here, we fit a linear model to predict the change in total food received (difference in food received per trial) when key donors were removed. Number of *nonkin females fed* in the past 4 years was a predictor representing investment in the size of a social support network. We did not count kin fed because this depended on the number of kin available. We did not count males fed because stable bonds in the wild are female-female. To control for sampling bias, we included the control variable *opportunity to donate*, which is the number of trials where the subject could have fed another bat (see supplement). The distribution of residuals did not deviate from normal (Shapiro Wilk's test: $W=0.98$, $p=0.95$). To visualize results, we plotted mean food received against *residual past sharing to nonkin females*—the residuals from a regression of the number of unrelated females fed on number of opportunities to donate (to control for the latter).

Results

Under typical conditions, when key donors were present, the number of female nonkin fed in previous years did not predict the amount of food received; instead the trend was negative (Fig. 1a; $R^2=0.43$, $\beta=-52.4$, $t=-1.81$, $p=0.155$). However, feeding more female nonkin did predict receiving more food later when a female's key donor was absent (Fig. 1b; $R^2=0.56$, $\beta=56.0$, $t=3.68$, $p=0.004$). A bat's proclivity to invest in female nonkin therefore predicted the *change* in total food she received when key donors were removed ($R^2=0.58$, $F(2,11)=7.54$; $\beta=108.4$, $t=3.48$, $p=0.005$; Fig. 1c). Females that fed more female nonkin coped better with partner removal. This result was robust to several variations in the analysis (see supplement).

Discussion

Our results provide further evidence that reciprocity plays a key role in vampire bat food sharing [8], and support the social bet-hedging hypothesis. By helping nonkin, individuals appear to maintain a wider support network than would be possible through only helping close kin. This suggests that female vampire bats can reduce the costs of losing a key donor by “not putting all their eggs in one basket.”

The social bet-hedging hypothesis makes three key assumptions. First, it assumes that individuals shift cooperative investments to and from individuals based on their relative cooperative returns, as predicted by reciprocity and biological market theory (e.g. models of partner control and partner choice) [1-3].

Second, it assumes not only that there are fitness benefits to having both more cooperative partners and stronger relationships [11-17], but that individuals often face a tradeoff between investing in relationship quantity versus quality (strength). If cooperative relationships require continuous investment, then merely increasing the number of weak connections can reduce overall cooperative returns, just as increasing offspring production at the expense of offspring quality does not reliably increase fitness [18]. On the other hand, strengthening each relationship can come at the expense of relationship quantity, so individuals might therefore divert investments towards partners that yield lower indirect fitness or reciprocal returns simply to create more relationships.

Third, social bet-hedging only makes sense if lost cooperative partnerships cannot be replaced instantly and effortlessly (as evidenced by Fig. 1a). Backup partners must already be in place. Social bet-hedging therefore assumes that new relationships require time and energy to develop. This seems true for food-sharing vampire bats [5-10].

Social bet-hedging may also exist for other cooperative behaviors. For example, female baboons increase their social grooming rates and groom more partners after the death of a close female relative [20], suggesting that investments in more relationships can help to compensate for the loss of a key social partner. In humans, although relationship quality is better than relationship quantity at predicting received social support [21], people appear to benefit from a greater number of weaker friendships in environments where friends are more likely to leave [22].

Many models of cooperation focus on pairwise interactions [e.g. 2], but cooperative “exchange rates” are determined by the supply and demand of cooperative services and partners—properties of the larger social network [19]. Many cooperative species might allocate cooperative investments across several partners and compare the varying return rates from each [3, 19]. It remains unclear, however, if or how different social animals balance the quality and quantity of social ties. By influencing the number and strength of connections in a social network, strategies like social bet-hedging can both shape, and be shaped by, social network structure.

Ethics statement

All procedures were approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-10-63).

Data accessibility

The data supporting this article have been uploaded as part of the online supplement.

Competing interests

We have no competing interests.

Authors' contributions

GGC and DF conceived of the analysis, GGC carried out the analysis, and DF and GSW advised the analysis. GGC drafted the manuscript; DF and GSW revised it critically for important intellectual content. All authors gave final approval of the version to be published, and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Acknowledgements

We thank the Organization for Bat Conservation for their extraordinary support. Rachel Crisp, Julia Vrtilek, and two anonymous reviewers provided comments that improved the manuscript.

Funding

Work by GGC was supported by a Ford Predoctoral Fellowship, a Dissertation Improvement Grant from the National Science Foundation (IOS-1311336), and grants from the American Society of Mammalogists and Animal Behavior Society.

References

- 196 [1] Trivers, R.L. 1971 The evolution of reciprocal altruism. *Quarterly Review of Biology*.
197 **46**, 35-57.
- 198 [2] Axelrod, R. & Hamilton, W.D. 1981 The evolution of cooperation. *Science* **211**,
199 1390-1396.
- 200 [3] Noë, R. & Hammerstein, P. 1994 Biological markets: supply and demand determine
201 the effect of partner choice in cooperation, mutualism and mating. *Behavioral*
202 *Ecology and Sociobiology* **35**, 1-11.
- 203 [4] Philippi, T. & Seger, J. 1989 Hedging one's evolutionary bets, revisited. *Trends in*
204 *Ecology & Evolution* **4**, 41-44.
- 205 [5] Carter, G.G. & Wilkinson, G.S. 2013 Food sharing in vampire bats: reciprocal help
206 predicts donations more than relatedness or harassment. *Proceedings of the Royal*
207 *Society of London B* **280**, 20122573.
- 208 [6] Carter, G.G. & Wilkinson, G.S. 2015 Social benefits of non-kin food sharing by
209 female vampire bats. *Proceedings of the Royal Society of London B* **282**,
210 20152524-20152524.
- 211 [7] Wilkinson, G.S. 1984 Reciprocal food sharing in the vampire bat. *Nature* **308**, 181-
212 184.
- 213 [8] Carter, G.G. & Wilkinson, G. 2013 Does food sharing in vampire bats demonstrate
214 reciprocity? *Communicative and Integrative Biology* **6**, e25783.
215 (doi:10.4161/cib.25783).
- 216 [9] Wilkinson, G.S. 1988 Reciprocal altruism in bats and other mammals. *Ethology and*
217 *Sociobiology* **9**, 85-100.

- 218 [10] Wilkinson, G.S. 1985 The social organization of the common vampire bat: I. Pattern
219 and cause of association. *Behavioral Ecology and Sociobiology* **17**, 111-121.
- 220 [11] Kokko, H., Johnstone, R.A. & Clutton-Brock, T.H. 2001 The evolution of
221 cooperative breeding through group augmentation. *Proceedings of the Royal*
222 *Society of London B* **268**, 187-196.
- 223 [12] Seyfarth, R.M. & Cheney, D.L. 1984 Grooming, alliances and reciprocal altruism in
224 vervet monkeys. *Nature* **308**, 541-543.
- 225 [13] Seyfarth, R.M. & Cheney, D.L. 2012 The evolutionary origins of friendship. *Annual*
226 *Review of Psychology* **63**, 153-177.
- 227 [14] Seyfarth, R.M., Silk, J.B. & Cheney, D.L. 2014 Social bonds in female baboons: the
228 interaction between personality, kinship and rank. *Animal Behaviour* **87**, 23-29.
- 229 [15] Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R.,
230 Wittig, R.M., Seyfarth, R.M. & Cheney, D.L. 2009 The benefits of social capital:
231 close social bonds among female baboons enhance offspring survival.
232 *Proceedings of the Royal Society of London B* **276**, 3099-3104.
- 233 [16] Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R.,
234 Wittig, R.M., Seyfarth, R.M. & Cheney, D.L. 2010 Strong and consistent social
235 bonds enhance the longevity of female baboons. *Current Biology* **20**, 1359-1361.
- 236 [17] Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M. & Cheney,
237 D.L. 2008 Focused grooming networks and stress alleviation in wild female
238 baboons. *Hormones and Behavior* **54**, 170-177.
- 239 [18] Smith, C.C. & Fretwell, S.D. 1974 The optimal balance between size and number of
240 offspring. *The American Naturalist* **108**, 499-506.

- [19] 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.
- [20] Engh, A.L., Beehner, J.C., Bergman, T.J., Whitten, P.L., Hoffmeier, R.R., Seyfarth, R.M. & Cheney, D.L. 2006 Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society of London B* **273**, 707-712.
- [21] Franks, H.M., Cronan, T.A. & Oliver, K. 2004 Social support in women with fibromyalgia: Is quality more important than quantity? *Journal of Community Psychology* **32**, 425-438.
- [22] Oishi, S. & Kesebir, S. 2012 Optimal social-networking strategy is a function of socioeconomic conditions. *Psychological Science*, 0956797612446708.

Figure Legends

Figure 1. Bats with a higher propensity to help unrelated females suffered smaller losses in total food received when a key donor was removed as a potential donor.

Proclivity to feed more nonkin females (x-axis) did not positively correlate with food received when a non-donor was absent (panel a) but it did when the key donor was absent (panel b). Feeding more unrelated females predicted smaller reductions in food received when the key donor was removed (panel c). Shading shows 95% confidence interval of the slope.