



Food sharing in vampire bats is explained by past help more than relatedness or harassment

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Background

Cooperation poses an evolutionary puzzle whenever donors pay a cost to help a recipient. The puzzle is that natural selection would favor “cheats” that gain the fitness benefits of cooperation without paying the costs. For cooperation to be evolutionarily stable, such “cheating” must therefore be prevented.



Common vampire bats feed only on blood and die after about 72 hours without food. However, **unfed bats often receive regurgitated food from roost-mates**. Vampire bat food sharing can provide insight into how cheating is prevented in a cooperative society because this helping behavior is natural, costly to donors, occurs between kin and non-kin, and can be induced experimentally.

Previous work [1] showed that **food sharing in free-ranging vampire bats was predicted equally and independently by co-roosting association and genetic relatedness**. Female vampire bats shared food most often with their own offspring, but also with related and unrelated adult females of high association. A captive fasting experiment provided evidence that unrelated bats directed donations to their past donors on 4 of 6 occasions– more than expected by chance.

Hypotheses

The original findings were interpreted as evidence that cheating is prevented by both direct reciprocity and kin discrimination. **This hypothesis predicts that past reciprocal help and kinship should be the best predictors of future food donations.**

Authors have proposed 3 alternative explanations for vampire bat food sharing, each of which makes distinct predictions. **The harassment hypothesis [2] predicts that unfed bats, not donors, will initiate food sharing by persistent begging, and donations will be directed primarily to dominant individuals.** It is also possible that non-kin food sharing is an error or byproduct of kin selection. **The miscalibrated kin recognition hypothesis [3] predicts that donors should donate almost exclusively to kin when in the presence of both kin and non-kin, regardless of the donor’s past experience of help.** Finally, it is possible that non-kin food sharing results from kin selection that operates based on group-membership (equivalent to predictions of a multi-level selection model). **The group-level altruism [4] hypothesis predicts that donors will help all group members indiscriminately, regardless of past help or relatedness.**

We tested the predictions of the above hypotheses by experimentally simulating 52 unsuccessful foraging attempts in a captive colony of 25 common vampire bats (*Desmodus rotundus*) of mixed relatedness and equal familiarity. Under conditions of equal co-roosting association, we directly compared predictors of food donated across dyads including relatedness and food received.

Methods

Behavioral data

To induce food sharing we removed a subject from the colony and fasted it for 24 h, then returned it to fed colony-mates, and recorded subsequent interactions with all other bats for 2 h with a digital camcorder and infrared illumination. We measured the subject’s mass immediately before reintroduction and after the 2 h observation period. We randomly selected bats without replacement to serve as subjects, with each subject tested 1-5 times. We tested 11 adult males, 9 adult females, and 3 young of the year.

We measured allogrooming through random focal sampling. We used mouth-licking time to estimate amount of food shared because mouth-licking time strongly correlated with immediate subsequent mass gain in a trial (r=0.90; 95% C.I.=0.73 – 0.96). Wherever an opportunity existed for food sharing in each direction, we pooled time spent donating food from multiple days to obtain a single measure of food sharing for each directional dyad (n=312), except when we analyzed sharing events over time.

Pairwise relatedness

We extracted DNA from 2-3 mm biopsy punches using Qiagen DNeasy kits, then amplified and genotyped 13 microsatellite loci using sequences available in GenBank. We used the program ML-RELATE to calculate maximum likelihood pairwise relatedness. We jackknifed across the 13 loci to estimate standard errors (SE) of individual pairwise relatedness values: SE range=0-0.035 (SE mean=0.005). Maximum likelihood estimates for pairwise coefficients of relatedness (r) were

Pairwise r	% of directional dyads
0 – 0.04	69%
0.05 – 0.24	11%
> 0.25	20%

Statistical analysis

We therefore defined “food donated” as

$$\ln \frac{\text{total food given from bat A to B} + 1}{\text{chances for bat A to feed B}}$$

and “food received” as the same value with the roles of bat A and B reversed. We then z-transformed all variables to standardize scales.

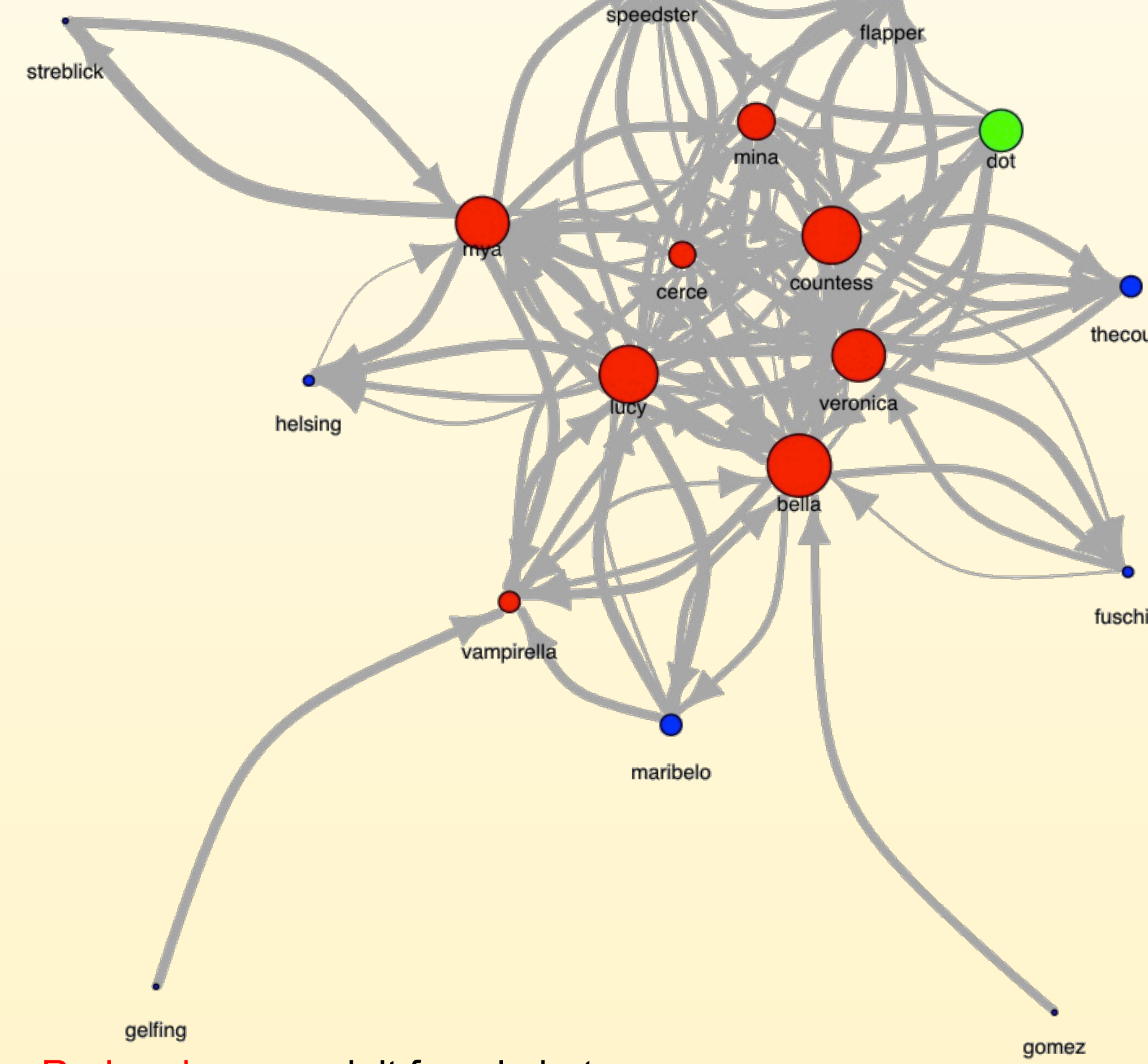
To analyze dyadic data we used a randomization approach to general linear models, where we permuted food donated to sets of predictor variables. We first conducted univariate analyses to identify variables that predicted mean food donated across dyads, testing both the original and transformed values. We then conducted permuted multiple regressions using the lmp function in the lmpPerm package implemented in R.

To determine if individual food donations were exchanged in a reciprocal manner over time, we also examined the sequence of sharing events across trials.

Finally, to assess the harassment hypothesis, we examined whether donations were more often recipient-initiated or donor-initiated, and tested two potential measures of coercion ability: recipient age and size (forearm length) as potential predictors of food donated.

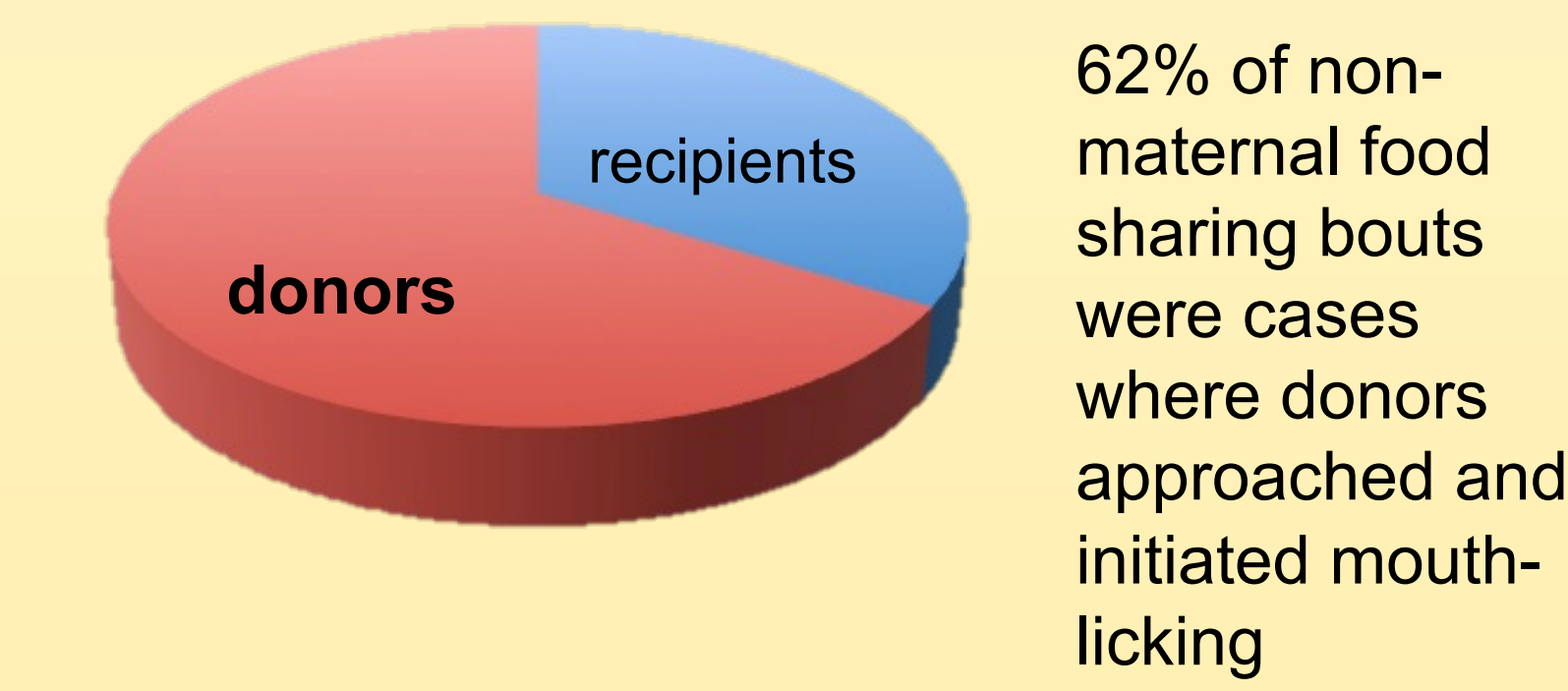
Results

Food sharing network

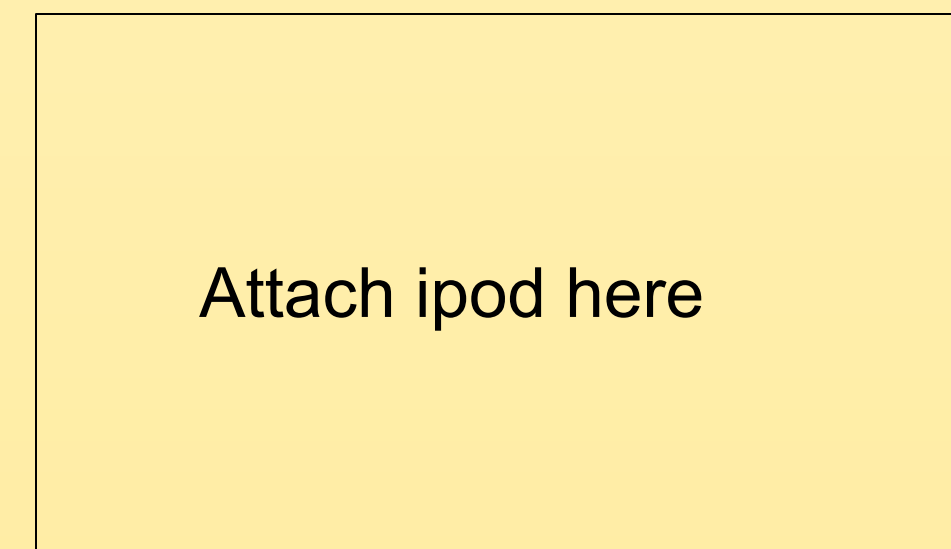


Red nodes are adult female bats
Blue nodes are adult male bats
Green nodes are young of the year bats
Grey arrows show direction of food donation
Width of arrow is log-transformed amount donated
Size of node shows number of partners fed
98 donations total
Spatial layout based on fruchterman-reingold algorithm

Who initiated food sharing?



Video of food sharing initiated by donor



Pattern of food sharing

- Unfed adult females and juveniles were always given food
- Food sharing never occurred between adult males
- 63 of 98 food sharing dyads had relatedness estimates less than 0.05 (64% expected if dyads were formed randomly with respect to kinship)
- 1-7 donors per fasting trial (mean=3.9)
- Food sharing restored ~20% of mass lost from 24 h of fasting

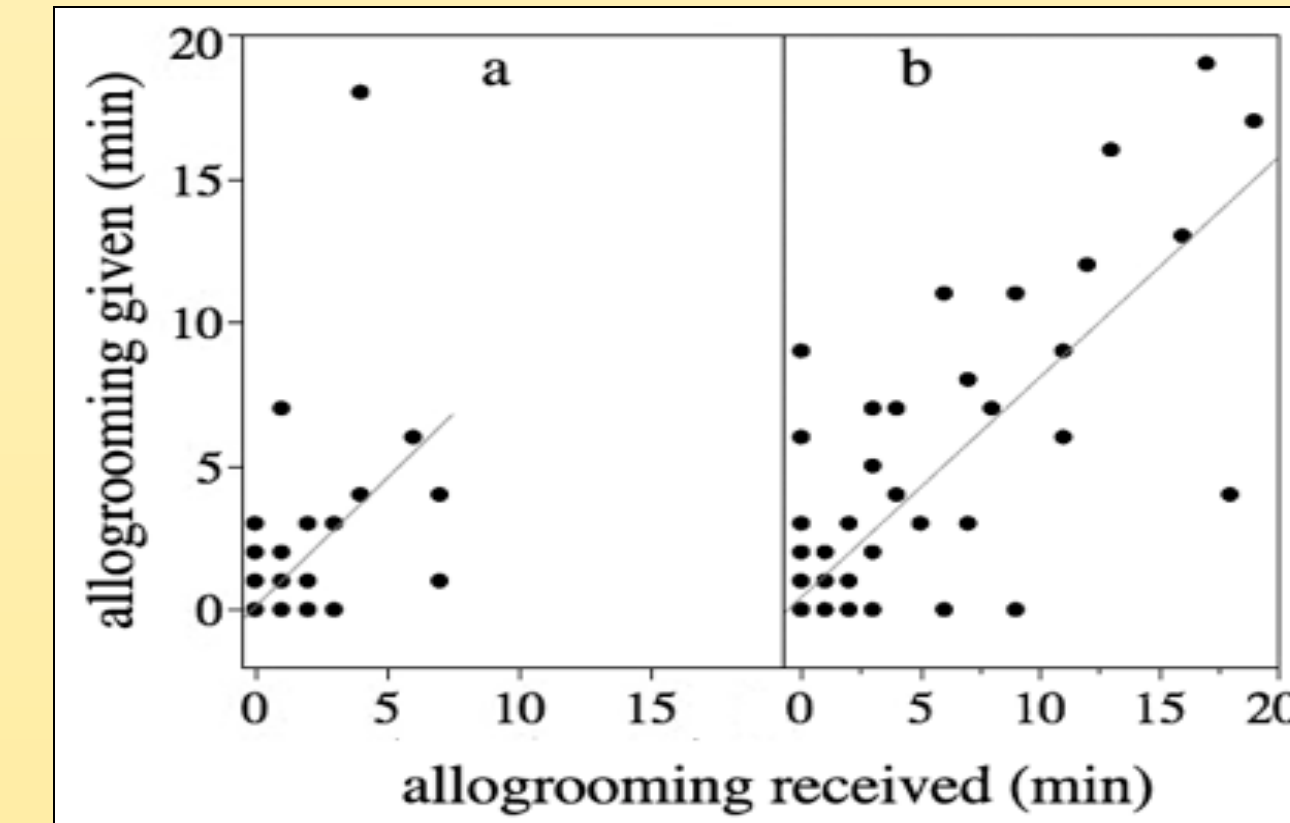
Predictors of food sharing

Variable	coefficient	p-value
Past food received from recipient	0.319	<0.0002
Donor sex	0.267	<0.0002
Allogrooming from recipient	0.186	<0.0002
Interaction: kinship and food received	0.069	0.0276

Full model, adj. R²= 0.37, F(5,306)=37.8 p<0.0002

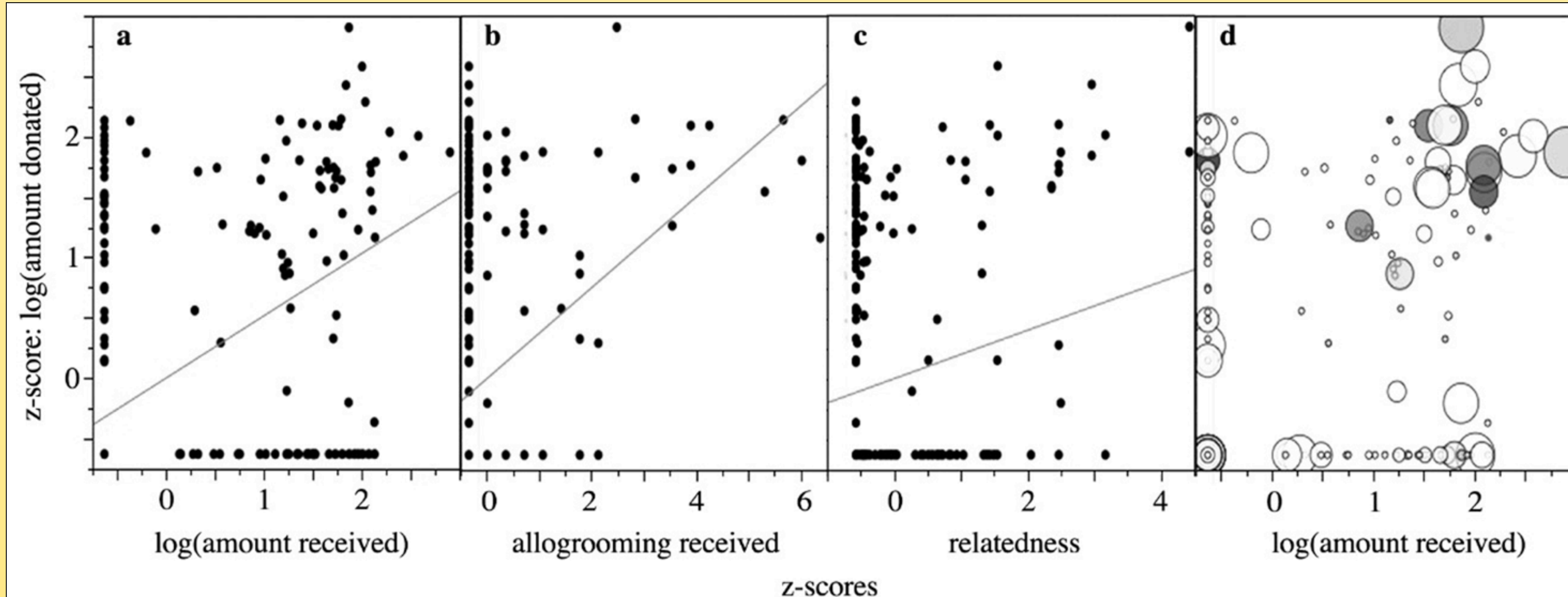
- Linear relationship between food donated and received increased in steepness with higher relatedness
- Food received was 8.5 times more important than relatedness for predicting food sharing
- Food received also predicted proportion of donor’s contribution to present partner over time (p<0.0002)
- No evidence of generalized reciprocity or an effect of recipient age or size
- Food sharing network (above) was consistent over 8 days (p=0.0072) or 6 months (p<0.0002).
- Food sharing dyads performed more allogrooming than non-food sharing dyads (F(1,310)=41, p<0.0002).

Mutual allogrooming



Allogrooming given and received was correlated for (a) non-sharing (n=214, r=0.62, p<0.0002) and (b) food sharing dyads (n=98, r=0.810, p<0.0002).

Univariate analyses: predictors of donation size



Z-scores for log mean amount of food donated were predicted by z-scores of (a) log mean amount of food received (R²=0.27), (b) allogrooming received (R²=0.14), and (c) relatedness (R²=0.04). A bubble plot (d) illustrates the multivariate relationships by scaling bubble size by relatedness and darkness by allogrooming received.

Conclusions

Past social experience of help is the most important predictor of food sharing in vampire bats under controlled conditions of equal familiarity and mixed relatedness.



Mutual food sharing and social grooming over time suggest an important role for long-term social bonds.

Harassment hypothesis was not supported. Donors, not unfed bats, were more likely to initiate food sharing. Recipient size or age did not predict food sharing.

The miscalibrated kin recognition hypothesis was not supported. Non-kin food sharing prevails in a captive colony of mixed relatedness. Relatedness did not predict the presence or amount of food sharing across dyads that could have shared food.

The group-level altruism hypothesis was not supported. The network of allogrooming relationships and food donations within the captive group was non-random and more consistent over days and months than expected by chance.

Reciprocity was supported but not demonstrated. Together with past findings [1], our data suggest that non-kin food sharing is unlikely to be explained by harassment or kin recognition errors. Although this study suggests there are direct benefits of food sharing, **experiments testing if and how donors respond to cheating are needed** to demonstrate reciprocity if it indeed enforces cooperation.

We found that fasted bats were fed by an average of three donors, suggesting that the costs of food sharing were often divided among partners.

Surprisingly, fasted subjects sometimes appeared to reject food offers from potential donors. This unexpected observation indicates that **bats might favour some individuals as partners over others, which has implications for modelling vampire bat cooperation as a social market [e.g. 5] rather than as a repeated dyadic interaction.**

References

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