

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

Title:

Development of new food-sharing relationships among nonkin vampire bats

Authors and affiliation:

Gerald G. Carter^{1,2}, Damien R. Farine^{3,4,5,6}, Rachel J. Crisp^{2,7}, Julia K. Vrtilek^{2,8}, Simon P. Ripperger^{1,2,9}, Rachel A. Page²

¹Department of Ecology, Evolution, and Organismal Biology; The Ohio State University, Columbus, OH, USA

²Smithsonian Tropical Research Institute, Balboa, Ancón, Panamá

³Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, UK

⁴Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany

⁵Chair of Biodiversity and Collective Behaviour, Department of Biology, University of Konstanz, Konstanz, Germany

⁶Center for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

⁷Centre for Research in Animal Behaviour, University of Exeter, Exeter, UK

⁸Department of Biology, Eidgenössische Technische Hochschule Zürich, Zürich, Switzerland

⁹Museum für Naturkunde, Leibniz-Institute for Evolution and Biodiversity Science, Berlin, Germany

Corresponding author:

Gerald Carter, 318 W. 12th Avenue, 300 Aronoff Laboratory, Columbus, OH 43210, carter.1640@osu.edu

23 **Abstract**

24 Social relationships that involve costly helping occur most often among kin, but in many
25 complex and individualized animal societies, nonkin also demonstrate stable cooperative relationships
26 that share similarities with human friendship. How do such cooperative bonds form between complete
27 strangers? Here, we show evidence that unfamiliar nonkin vampire bats (*Desmodus rotundus*) selectively
28 escalate low-cost investments in allogrooming before developing higher-cost food-sharing relationships.
29 By introducing female bats from geographically distant sites in captive pairs or groups and fasting them
30 repeatedly over 15 months, we observed that increasing rates of grooming a partner predicted the
31 occurrence of that partner's first food donation back to the groomer, after which grooming rates no
32 longer increased. New food-sharing relationships formed in 14.5% of 608 possible female pairs,
33 emerged in a reciprocal pattern, and developed more often when strangers lacked alternative familiar
34 partners. Our results are consistent with predictions from the 'raising-the-stakes' hypothesis that
35 strangers 'test the waters' of new relationships by initially making low-cost investments in grooming
36 before making higher-cost food donations. This form of 'raising the stakes' (e.g., transitions from
37 clustering to grooming to food sharing) might play an underappreciated role in many other social
38 decisions with long-term consequences, such as joining a new social group or choosing a long-term
39 mate.

40 **Keywords:** cooperation, social relationships, vampire bats

41

42 **Significance statement**

43 Vampire bats form long-term cooperative social bonds that involve reciprocal regurgitated blood
44 sharing. But how do two individuals go from complete strangers to reciprocal food donors? By
45 introducing unfamiliar bats, we found evidence that low-cost grooming paves the way for higher-cost
46 food donations. Bats that formed new food-sharing relationships had a history of escalating reciprocal
47 grooming up until the food sharing began. Food sharing emerged in a reciprocal fashion and it emerged
48 more often when two strangers could not access their original groupmates. The finding that unfamiliar
49 nonkin vampire bats appeared to gradually and selectively transition from low-cost to high-cost
50 cooperative behaviors is the first evidence that nonhuman animals 'raise the stakes' when forming new
51 cooperative relationships.

52

53

54 **Text**

55 Animal societies are fundamentally shaped by repeated interactions among individuals over
56 time. Repeated interactions allow individuals to choose to cooperate based on their past experience
57 across different partners (1-3). Organisms as diverse as animals, plants, and fungi have demonstrated
58 partner choice: individuals prevent exploitation by shifting their cooperative investments towards
59 partners that provide better reciprocal returns (3-7). Across several nonhuman mammals, repeated
60 cooperative interactions lead to adaptive and enduring social bonds that share similarities with human
61 friendship (8-12), but it remains unclear how these initially form. A significant challenge has been
62 understanding how individuals prevent exploitation while forming these stable bonds. How do complete
63 strangers develop a long-term cooperative relationship?

64 A key idea is that individuals should reduce the risk of exploitation by initially spreading out
65 smaller cooperative investments across time ('parceling' (13)) or across different partners ('social bet-
66 hedging' (14)), and then gradually escalating investments in the most cooperative partnerships ('raising
67 the stakes' (15)). For example, one might first assess a potential partner's tolerance by clustering for
68 warmth, then gain feedback by grooming the partner, and then use the partner's response to decide
69 whether to provide higher-cost food donations or coalitionary support (16). Despite its intuitive appeal
70 for explaining how new cooperative relationships develop, evidence supporting the 20-year-old 'raising-
71 the-stakes' model (15) is surprisingly scarce. An early test using the cleaner and client fish mutualism
72 suggested that the model does not apply well to situations with severe asymmetries in partner payoffs or
73 options (17). Studies with nonhuman primates (18-21) have tested only snapshots of established
74 relationships rather than the formation of new ones. Human strangers 'raise the stakes' when making
75 monetary bids in cooperation games (e.g. 22, 23), but we currently lack supporting evidence for this
76 strategy in the more ecologically-relevant context of relationship formation. Gathering this evidence
77 requires measuring the emergence of natural helping behaviors between randomly introduced strangers.

78 We tracked the development of new cooperative relationships between previously unfamiliar
79 wild-caught vampire bats (*Desmodus rotundus*) over 15 months. Cooperative relationships in this
80 species involve low-cost allogrooming (hereafter *grooming*) and higher-cost regurgitations of ingested
81 blood, or *food sharing* (14, 24-28). We found support for several lines of evidence that vampire bats use
82 reciprocal grooming to gradually establish new bonds that include food donations. If bats choose
83 partners, then new food-sharing relationships should form more often when bats have fewer alternative
84 partners. If grooming gradually leads to sharing, then grooming rates should predict the probability that
85 the grooming recipient later donates food back to the groomer. Grooming rates should also start low
86 and increase over time but only up until the first reciprocal food donation. Finally, new food sharing
87 should be rarer, occur after mutual grooming, and emerge in a reciprocal fashion.

88 Female vampire bats demonstrate kin-biased fission-fusion social dynamics (24, 27, 28). New
89 nonkin social bonds can form when an unrelated female joins a social network about once every two
90 years (24, 28), with individual bats living for up to 16 years in the wild (29). To observe how new food-
91 sharing relationships form between adults, we captured adult females from two distant sites in Panamá,
92 Tolé (n=19) and Las Pavas (n=8), and we then ran 638 fasting trials in which an overnight-fasted subject
93 could be fed by a previously unfamiliar bat from another site. To test the prediction that new sharing
94 relationships would form more often when strangers have fewer partner options, we compared the
95 occurrence of new sharing when wild-caught strangers were introduced in isolated pairs (one Las Pavas
96 and one Tolé bat), in small groups (one Las Pavas and three Tolé bats), or in one large mixed group (all
97 bats together; see Methods, Supplementary Information (SI) Appendix, Fig. S1). New bonds can also
98 form when individuals are born into a group, and these relationships might form differently. We therefore
99 also measured the development of non-maternal cooperative relationships between 26 female adults
100 and 13 younger captive-born bats (6 males and 7 females, 11 to 21 months old) in the large mixed
101 group.

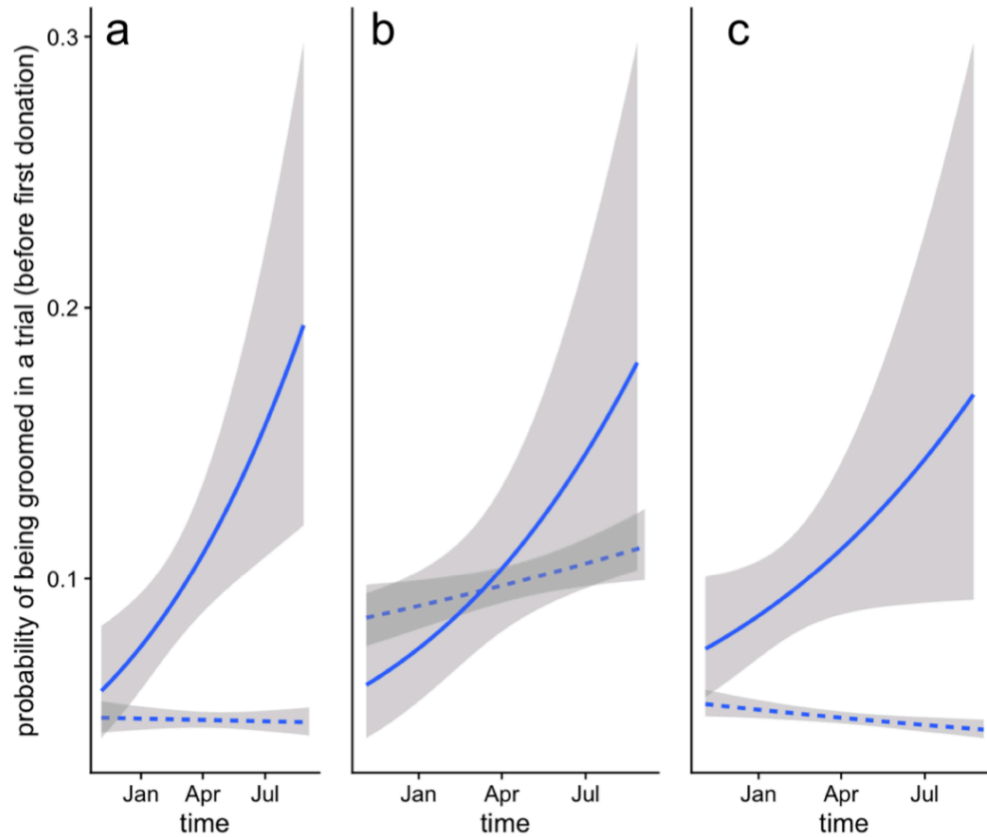
102 To test our hypotheses, we compared the observed coefficients from general and generalized
103 linear models (slopes β , and odds ratios OR, respectively) to expected distributions of coefficient values
104 expected under the null hypotheses using permutations of the network or the event data (see Methods).
105 We use the term 'potential relationship' for a pair of bats that could have groomed or shared food, the
106 word 'relationship' for an *observed* network edge (directed), and the word 'bond' to discuss the
107 underlying construct that we *inferred* from the observed relationship (see SI, Table S1).

108 Fasted bats were fed by at least one donor in 61% of trials (SI Appendix 2). Over 424 days and
109 12,012 opportunities for new food donations, new food sharing developed in 10.8% of the 996 potential
110 relationships among all bats, 14.5% of 608 potential relationships among females, and 15.6% of 243
111 potential relationships among wild-caught adult females (SI Appendix 3). All bats had at least one donor
112 (range=1-16, mean=6.6). The average number of new food donors per adult female bat was 2.7
113 (range=0-7) and the average per captive-born bat was 2.6 (range=0-6). New grooming relationships
114 developed far more frequently (all bats=51.9% of 1008; females=58.9% of 618; wild-caught adult
115 females=78.2% of 248). The average number of new groomers was 7.2 (range=0-16) for adult females
116 and 14.4 (range=1-23) for captive-born bats.

117 If bats choose new partners based on their phenotype alone, then relationships should form
118 more often when bats have more alternative partners. On the other hand, if bats ‘test the waters’ of each
119 new relationships, they should choose partners based on both the availability of different partners and
120 their past experiences with each, and food-sharing relationships should therefore form more often when
121 bats have *fewer* alternative partners. As expected, when strangers from Las Pavas and Tolé were
122 introduced and housed as isolated pairs, we observed higher rates of new food sharing ($\beta=1.14$,
123 $p=0.002$) and new grooming ($\beta=1.09$, $p=0.02$) compared to when one Las Pavas bat was introduced to
124 three Tolé bats, despite there being fewer potential new bonds available to form (SI Appendix 4). When
125 we aggregated bats from the controlled introduction trials into a large mixed group, bats preferentially
126 fed and groomed their original familiar groupmates, and new sharing emerged even more gradually than
127 in the isolated pairs or in small groups (SI Appendix 5, Fig. S2 and S3).

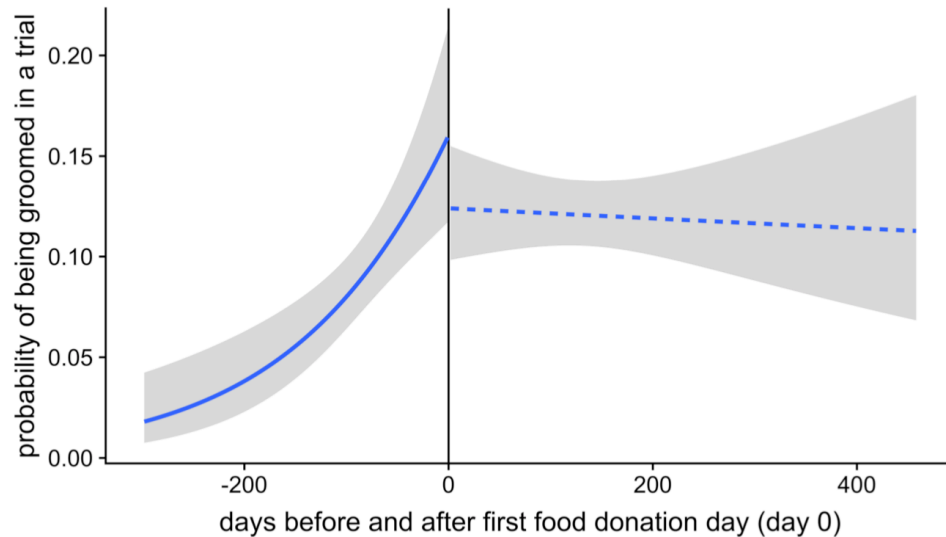
128 If the bats use low-cost grooming to build higher-cost sharing bonds, then the grooming rate
129 should predict the probability of the first food donation in the opposite direction. As expected, new food
130 sharing emerged on days after we observed mutual grooming more than expected by chance (SI
131 Appendix 6), and the grooming rate given by actor A to recipient B predicted the later occurrence of new
132 food sharing from B back to A (OR=2.15, $p=0.0002$, $n=897$). The trajectory of grooming rates over time
133 clearly differed between pairs that developed new food-sharing relationships versus pairs that did not
134 (interaction: OR=1.60, $p<0.0001$, Fig. 1). The slope of this increase in grooming was also greater *before*
135 the first reciprocal food donation than after. Initial grooming rates started low, then increased over time
136 up until the new food-sharing relationship formed (Fig. 2).

137
138



139
140
141
142
143
144
145
146
147
148

Fig. 1. Increasing A-to-B grooming led to new B-to-A food-sharing relationships. In cases where a new food-sharing relationship formed (solid line), the grooming rate towards the future donor increased over time before the first donation occurred (OR=1.40, n=33, $p<0.0001$), but the grooming rate towards a potential donor remained low in cases where no food-sharing relationship formed (dashed line; OR=0.99, n=420, $p=0.58$). This divergence in all potential new relationships (panel a) was also detected within previously unfamiliar adults (panel b), and within relationships with captive-born bats (panel c), which had more divergent grooming trajectories (SI Appendix 7). Shading shows the 95% CI for the fitted model's predictions.



149
150 **Fig. 2. Grooming rates increased before, but not after, new food-sharing occurred.** The probability
151 of a focal bat grooming the new donor in a 1-h trial (y-axis) increased before the first day that the donor
152 fed the focal bat (i.e. 'day zero'; OR=1.4, $p=0.0005$), but not after this day zero (OR=1.01, $p=0.47$;
153 interaction: OR=1.57, $p=0.0003$). This effect was seen in new food-sharing relationships with or without
154 captive-born bats (SI Appendix 8). Shading shows the 95% CI for the fitted model's predictions.
155

156 Emergence of new food sharing was more reciprocal than expected by chance, even when
157 controlling for kinship (MRQAP-DSP; reciprocal sharing: $\beta=0.33$, $p<0.0002$, kinship: $\beta=0.02$, $p=0.65$; SI
158 Appendix 9). Grooming rates in new relationships were also symmetrical across dyads but we lacked the
159 power to determine whether grooming symmetry increased over time within dyads (see SI Appendix 10).
160 Grooming rates were highest between bats that formed two-way food-sharing relationships,
161 intermediate in relationships where we observed sharing in only one direction, and lowest in pairs where
162 we never saw food sharing (SI, Fig. S4).

163 The rarity of new food-sharing relationships corroborates past evidence that food regurgitations
164 are energetically costly and that food-sharing bonds require investments of time and energy (14, 24, 30,
165 31). The relationship between new grooming and new food sharing was unlikely to be caused by mere
166 proximity because the effect of new grooming on new food sharing remained evident regardless of
167 whether or not bats were forced into close proximity (SI Appendix 11).

168 These findings provide the clearest evidence to date that nonkin food sharing in vampire bats is
169 not a byproduct of kin selection (26). Before this study, one hypothesis was that food sharing decisions
170 among nonkin could depend entirely on heuristics based on phenotypic similarity, resulting in a spurious
171 pattern of symmetrical helping that looks like reciprocity (32, 33). However, this hypothesis incorrectly
172 predicts that food-sharing relationships should form immediately and occur most frequently in larger
173 groups simply because there are more opportunities for similar matching phenotypes.

174 Our results were consistent with the hypothesis that relationships formation occurs through
175 some form of 'raising the stakes' (15). This model has yet to be tested during the transition from
176 'strangers' to 'friends' because these changes are difficult to document in nature (see SI Appendix 12).
177 Past evidence for the 'raising-the-stakes' strategy (15) has also been scarce in part because it is a
178 variation on the classic 'tit-for-tat' strategy in the iterated prisoner's dilemma (1), a model which is
179 difficult to test using natural forms of cooperation (4, 32, 34). 'Tit-for-tat' forms of reciprocity are
180 demonstrated by experiments with trained instrumental tasks and payoffs that accrue in distinct rounds,
181 such as rats taking turns to pull a lever to deliver food (4-6). However, the 'tit-for-tat' model excludes
182 many factors crucial in the real world, including partner choice, partner fidelity, exchange of multiple
183 service types, and the many cost-benefit asymmetries resulting from demography, market effects, and
184 social rank (4, 7, 34). If social bonding involves integrating many different kinds of social interactions into
185 a single positive association, one should not expect clearly alternating exchanges of help. In primates,

186 cooperation within long-term social bonds does not produce strict ‘tit-for-tat’ exchanges of help;
187 strongly bonded partners show *less* evidence for short-term contingencies in grooming (9).

188 To clearly demonstrate that an actor’s cooperative investments are contingent on a partner’s
189 previous behavior, one must prevent reciprocation and then detect a subsequent decrease in the actor’s
190 cooperative investment. This evidence of reciprocity has yet to be experimentally demonstrated in food-
191 sharing vampire bats or in any other long-term social relationship (SI Appendix 13). Our findings show
192 that such an experiment would be most powerful if researchers targeted newly developing relationships
193 rather than established ones, and if they tracked multiple cooperative behaviors rather than just one.
194 Past studies on ‘raising the stakes’ during relationship development have focused on increasing rates of
195 a single cooperative behavior (18-23), but individuals can also raise the stakes by adding new higher-
196 cost behaviors. Our findings suggest that female vampire bats do both, first increasing grooming rates
197 and then transitioning from low-cost grooming to high-cost food-sharing.

198 The relevance of our findings extends beyond high-cost cooperative behaviors. For example, in
199 some species, courtship behaviors could be seen as a short-term investment in the formation of longer-
200 term pair bonds with substantial fitness consequences (35). Similarly, the role of mere physical contact
201 as a low-cost method for building tolerance and trust might be more general than currently recognized.
202 The key role of grooming for relationship maintenance in primates is well established, but growing
203 evidence suggests that similar tactile behaviors can reduce fear and encourage tolerance and
204 cooperation in many other species of mammals, birds, and fish (e.g. 5, 36-42). Recently developed
205 methods for tracking formation of social bonds at fine temporal scales (43, 44) could provide new
206 opportunities to test whether gradual escalation of proximity and body contact is a widespread
207 mechanism for socially ‘testing the water’.

208

209 **Methods**

210 *Animals*

211 We conducted experiments at the Smithsonian Tropical Research Institute in Gamboa, Panama.
212 We used 41 common vampire bats (*Desmodus rotundus*) as subjects, including 19 female bats captured
213 exiting a roost in Tolé, Panamá; 8 female bats captured foraging at a cattle pasture in Las Pavas,
214 Panamá about ~215 km from Tolé; and 14 captive-born bats (8 females, 6 males). We studied adult
215 females and their young, because these individuals form the basis of food-sharing networks in the wild,
216 whereas adult males compete for access to territories and females and do not form stable bonds as
217 often (24-28). To ensure familiarity within groups and unfamiliarity between groups, we housed the
218 groups separately (Tolé bats for 6 months and Las Pavas bats for 2 weeks) before the study began. Bats
219 were marked with subcutaneous passive integrated transponders (Trovan Ltd. USA) and a visually
220 unique combination of forearm bands (Porzana, National Tag, and birdbands.com). To feed bats, we
221 provided refrigerated or thawed cattle or pig blood defibrinated with sodium citrate and citric acid.

222 We used a 3-4 mm biopsy punch to collect tissue samples in 80% or 95% ethanol, then used a
223 salt-chloroform procedure for DNA isolation, and a LI-COR Biosciences® DNA Analyser 4300 and the
224 SAGA GT allele scoring software to genotype individuals at 17 polymorphic microsatellite loci. Allele
225 frequencies were based on 100 bats from Tolé and 9 bats from Las Pavas, respectively. Genotypes were
226 99.9% complete. To estimate genetic relatedness, we used the Wang estimator in the R package
227 ‘related’. To estimate kinship, we assigned a zero kinship to known unrelated individuals from different
228 sites and to individuals with negative pairwise relatedness, and we assigned a kinship of 0.5 for known
229 mother-offspring pairs or pairs with genetic relatedness estimates greater than 0.5. For all other pairs,
230 we used genetic relatedness as the estimate for kinship.

231

232 *Experimental design*

233 We induced allogrooming and regurgitated food sharing using a fasting trial, in which a focal
234 subject was isolated from the group without food for a night and a day, then released back to the group
235 of fed bats for 1 hour the following night. During the hour, all grooming or food-sharing interactions with
236 the subject were recorded using an infrared (IR) light and an IR-sensitive video camera. Each food
237 sharing bout was estimated by the number of seconds that the unfed subject spent licking the mouth of
238 a particular groupmate. Grooming was defined as chewing or licking the fur or wings of another bat. The
239 dyadic sharing or grooming for a trial was estimated as the sum of all bouts that were at least 5 seconds

240 long. We weighed bats before and after trials. Observed mouth-licking durations predicted weight gain
241 (SI Appendix 1).

242 We conducted fasting trials in each group during three experimental phases (SI, Fig. S1). First, we
243 conducted 57 ‘baseline’ trials to assess preliminary sharing rates between the 19 Tolé bats housed in a
244 1.7 x 2.1 x 2.3 m outdoor flight cage (3,420 possible sharing interactions in one group). Second, we
245 conducted 106 ‘controlled introduction’ trials to assess possible formation of new food-sharing bonds
246 between bats introduced as either an isolated pair (one Las Pavas bat and one Tolé bat) or a quartet
247 (one Las Pavas bat and three Tolé bats), housed in a 28 x 28 x 40 cm clear plastic observation cage (10
248 pairs and 8 quartets). These controlled introductions provided for 162 opportunities for new food sharing
249 between previous strangers (SI, Table S2). Finally, we conducted 532 ‘mixed-group’ trials to assess the
250 formation of new sharing relationships when all bats were housed together in the flight cage described
251 above (19 Tolé, 7 Las Pavas, and 14 captive-born bats). The introductions in this combined group
252 provided 11,823 more opportunities for new sharing.

253

254 *Statistical analyses*

255 During the baseline and mixed-group trials, we estimated food donation size as the number of
256 seconds that a fasted subject spent mouth-licking a fed groupmate. During the controlled introduction
257 trials, however, when bats were forced in close proximity, we saw a greater frequency of begging,
258 defined as mouth-licking that is clearly not food-sharing because the partner is turning away from the
259 mouth-licking bat and the mouth-licking bat does not gain the weight that would be expected from food-
260 sharing. To be conservative when measuring sharing, we therefore did not count mouth-licking as food
261 sharing during the controlled introduction trials unless the subject weighed more than expected based
262 on the average weight change for bats that did not perform any mouth-licking.

263 Durations of sharing and grooming were lognormal. To create a standard index of grooming rates,
264 we therefore transformed the total duration of directed dyadic interactions in each trial using natural log
265 ($x+1$). We call these measures of the log duration per hour ‘rates’. When interaction bout duration and
266 probability had different meanings, we decomposed rates into two separate response variables:
267 amounts (the magnitude of nonzero rates in a trial) and probabilities (the presence or absence of a
268 nonzero rate in a trial). We used permutation tests with 10,000 permutations for p-values and
269 bootstrapping for all 95% confidence intervals. Null distributions were not always centered on zero due
270 to structure in the data, so caution must be taken when considering the observed coefficients.

271 Grooming could occur before sharing simply because it is more frequent. To test whether mutual
272 grooming preceded new sharing more than expected by chance, we compared the observed probability
273 of observing mutual grooming before new sharing to the values expected from a null model based on
274 randomly swapping the label of interactions (grooming versus sharing) within each dyad. This
275 permutation test controls for the relative frequency and timing of grooming and sharing events in new
276 dyads. To test for ingroup-outgroup biases in sharing for each site, we calculated observed coefficients
277 for the effect of the actor and receiver being from the same capture site on actor grooming rates, then
278 we calculated expected coefficients by permuting the grooming rates within each actor to different
279 possible recipients.

280 To test the effects of kinship and reciprocal grooming on the formation of new food-sharing
281 relationships in the mixed-group trials, we used multiple regression quadratic assignment procedure
282 with double semi-partialing (MRQAP-DSP) via the netlogit function in the sna R package. We also used
283 this method to test the effect of grooming on occurrence of new sharing only within the controlled
284 introduction trials. This procedure uses generalized linear models via the glm function in lme4 package
285 to calculate the observed coefficients and uses network-level permutations to get expected coefficients.
286 Since MRQAP-DSP cannot test interaction effects, we compared observed and expected interaction
287 coefficients using permutations in which we shuffled trial rates given by the actor among different
288 possible receivers and then shuffled the trial rates received by the receiver among different possible
289 actors. If the interaction coefficients were significant ($p < 0.05$), we conducted separate MRQAP-DSP
290 tests within each group.

291 To test whether interaction rates changed over time, we generated expected coefficients for
292 general or generalized linear models by permuting the order of interactions within each potential
293 relationship. One captive-born bat died for unknown reasons during the mixed-group trials, so we

294 removed it from all temporal analyses. To test for evidence of reciprocal sharing, we used MRQAP-DSP
295 to test if the matrix of new sharing in the mixed-group trials was predicted by reciprocal sharing when
296 controlling for kinship. As an additional test, we also counted the occurrence of both novel sharing and
297 reciprocal sharing for all new potential relationships, then counted the same number after randomizing
298 the presence of sharing across potential relationships.

299

300 *Data availability*

301 Behavioral data, genotypes, and R code are available as supplementary information.

302

303 **Acknowledgments**

304 We thank the Smithsonian Tropical Research Institute for logistical support. Isabelle Waurick conducted
305 the molecular lab work. Frieder Mayer enabled the molecular lab work. Work was supported by a
306 Smithsonian Postdoctoral Fellowship, a Humboldt Research Fellowship, a Smithsonian Institution
307 Scholarly Studies Grant and a grant from the National Geographic Society Committee for Research and
308 Exploration (WW-057R- 17).

309

310 **Author contributions**

311 Conceptualization, GC; Methodology, GC; Investigation, GC, RC, JV; Genotyping, SR; Statistical
312 analysis, GC; Original draft, GC; Review & Editing, GC, RC, JV, SR, DF, RP; Funding acquisition, GC,
313 SR, RP; Resources, RP; Supervision, GC, DF, RP;

314

315 **References**

- 316 1 Axelrod R & Hamilton WD (1981) The evolution of cooperation. *Science* 211:1390-1396.
- 317 2 Noë R & Hammerstein P (1994) Biological markets: supply and demand determine the effect of
318 partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* 35:1-11.
- 319 3 Trivers RL (1971) The evolution of reciprocal altruism. *Q. Rev. Biol.* 46:35-57.
- 320 4 Carter GG (2014) The reciprocity controversy. *Anim. Behav. Cogn.* 1(3):368-386.
- 321 5 Schweinfurth MK & Taborsky M (2018) Reciprocal trading of different commodities in Norway rats.
322 *Curr. Biol.* 28:1-6.
- 323 6 Rutte C & Taborsky M (2008) The influence of social experience on cooperative behaviour of rats
324 (*Rattus norvegicus*): direct vs generalised reciprocity. *Behav. Ecol. Sociobiol.* 62(4):499-505.
- 325 7 Fruteau C, Voelkl B, van Damme E, & Noë R (2009) Supply and demand determine the market value
326 of food providers in wild vervet monkeys. *Proc. Natl. Acad. Sci. USA* 106:12007-12012.
- 327 8 Samuni L, et al. (2018) Social bonds facilitate cooperative resource sharing in wild chimpanzees.
328 *Proc. R. Soc. B* 285(1888).
- 329 9 Seyfarth RM & Cheney DL (2012) The evolutionary origins of friendship. *Ann. Rev. Psych.* 63:153-
330 177.
- 331 10 Silk JB, et al. (2010) Strong and consistent social bonds enhance the longevity of female baboons.
332 *Curr. Biol.* 20(15):1359-1361.
- 333 11 Silk JB, et al. (2009) The benefits of social capital: close social bonds among female baboons
334 enhance offspring survival. *Proc. R. Soc. B* 276(1670):3099-3104.
- 335 12 Silk JB, Alberts SC, & Altmann J (2003) Social bonds of female baboons enhance infant survival.
336 *Science* 302(5648):1231-1234.
- 337 13 Connor RC (2010) Cooperation beyond the dyad: on simple models and a complex society. *Philos.*
338 *Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 365(1553):2687-2697.
- 339 14 Carter GG, Farine DR, & Wilkinson GS (2017) Social bet-hedging in vampire bats. *Biol. Lett.*
340 13(5):20170112.
- 341 15 Roberts G & Sherratt TN (1998) Development of cooperative relationships through increasing
342 investment. *Nature* 394(6689):175-179.
- 343 16 Borgeaud C & Bshary R (2015) Wild vervet monkeys trade tolerance and specific coalitionary
344 support for grooming in experimentally induced conflicts. *Curr. Biol.* 25(22):3011-3016.
- 345 17 Bshary R (2002) Building up relationships in asymmetric co-operation games between the cleaner
346 wrasse *Labroides dimidiatus* and client reef fish. *Behav. Ecol. Sociobiol.* 52(5):365-371.

- 347 18 Kaburu SS & Newton-Fisher NE (2013) Social instability raises the stakes during social grooming
348 among wild male chimpanzees. *Anim. Behav.* 86(3):519-527.
- 349 19 Barrett L, Henzi SP, Weingrill T, Lycett JE, & Hill RA (2000) Female baboons do not raise the stakes
350 but they give as good as they get. *Anim. Behav.* 59(4):763-770.
- 351 20 Manson JH, Navarrete CD, Silk JB, & Perry S (2004) Time-matched grooming in female primates?
352 New analyses from two species. *Anim. Behav.* 67(3):493-500.
- 353 21 Fruteau C, Lemoine S, Hellard E, van Damme E, & Noë R (2011) When females trade grooming for
354 grooming: Testing partner control and partner choice models of cooperation in two species of
355 primates. *Anim. Behav.* 81:1223-1230.
- 356 22 Roberts G & Renwick JS (2003) The development of cooperative relationships: an experiment. *Proc.*
357 *R. Soc. B* 270(1530):2279-2283.
- 358 23 Van den Bergh B & Dewitte S (2006) The robustness of the 'Raise-The-Stakes' strategy: Coping with
359 exploitation in noisy Prisoner's Dilemma Games. *Evol. Hum. Behav.* 27(1):19-28.
- 360 24 Wilkinson GS (1984) Reciprocal food sharing in the vampire bat. *Nature* 308:181-184.
- 361 25 Wilkinson GS (1986) Social grooming in the common vampire bat, *Desmodus rotundus*. *Anim.*
362 *Behav.* 34:1880-1889.
- 363 26 Carter GG & Wilkinson G (2013) Does food sharing in vampire bats demonstrate reciprocity?
364 *Commun. Integr. Biol.* 6(6):e25783.
- 365 27 Wilkinson GS (1985) The social organization of the common vampire bat. I. Pattern and cause of
366 association. *Behav. Ecol. Sociobiol.* 17:111-121.
- 367 28 Wilkinson GS (1985) The social organization of the common vampire bat: II. Mating system, genetic
368 structure, and relatedness. *Behav. Ecol. Sociobiol.* 17:123-134.
- 369 29 Delpietro H, Russo R, Carter G, Lord R, & Delpietro G (2017) Reproductive seasonality, sex ratio and
370 philopatry in Argentina's common vampire bats. *R. Soc. Open Sci.* 4(4):160959.
- 371 30 Carter GG & Wilkinson GS (2015) Social benefits of non-kin food sharing by female vampire bats.
372 *Proc. R. Soc. B* 282(1819):20152524-20152524.
- 373 31 Carter GG, Wilkinson GS, & Page RA (2017) Food-sharing vampire bats are more nepotistic under
374 conditions of perceived risk. *Behav. Ecol.* 28(2):565-569.
- 375 32 Clutton-Brock T (2009) Cooperation between non-kin in animal societies. *Nature* 462:51-57.
- 376 33 Hammerstein P (2003) Why is reciprocity so rare in social animals? A protestant appeal. *Genetic and*
377 *cultural evolution of cooperation* (ed. & Hammerstein P), pp. 83-93. Cambridge, MA: MIT Press.
- 378 34 Noë R (2006) Cooperation experiments: coordination through communication versus acting apart
379 together. *Anim. Behav.* 71:1-18.
- 380 35 Ihle M, Kempnaers B, & Forstmeier W (2015) Fitness benefits of mate choice for compatibility in a
381 socially monogamous species. *PLoS Biol.* 13(9):e1002248.
- 382 36 Kern JM & Radford AN (2018) Experimental evidence for delayed contingent cooperation among
383 wild dwarf mongooses. *Proc Natl Acad Sci U S A* 115(24):6255-6260.
- 384 37 Kenny E, Birkhead TR, & Green JP (2017) Allopreening in birds is associated with parental
385 cooperation over offspring care and stable pair bonds across years. *Behav. Ecol.* 28(4):1142-1148.
- 386 38 Grutter AS (2004) Cleaner fish use tactile dancing behavior as a preconflict management strategy.
387 *Curr. Biol.* 14(12):1080-1083.
- 388 39 Soares MC, Oliveira RF, Ros AF, Grutter AS, & Bshary R (2011) Tactile stimulation lowers stress in
389 fish. *Nat. Comm.* 2:534.
- 390 40 Schirmer A, Jesuthasan SJ, & Mathuru A (2013) Tactile stimulation reduces fear in fish. *Front. Behav.*
391 *Neuro.* 7:167.
- 392 41 Radford AN (2012) Post-allogrooming reductions in self-directed behaviour are affected by role and
393 status in the green woodhoopoe. *Biol. Lett.* 8(1):24-27.
- 394 42 Radford AN (2011) Preparing for battle? Potential intergroup conflict promotes current intragroup
395 affiliation. *Biol. Lett.* 7(1):26-29.
- 396 43 Alarcón-Nieto G, et al. (2018) An automated barcode tracking system for behavioural studies in
397 birds. *Meth. Ecol. Evol.* 9(6):1536-1547.
- 398 44 Ripperger S, Günther L, Wieser H, Duda N, Hierold M, Cassens B, Kapitza R, Koelpin A, & Mayer F
399 (2019) Proximity sensors on common noctule bats reveal evidence that mothers guide juveniles to
400 roosts but not food. *Biol. Lett.* 15(2):20180884.