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**Title:**

Development of new food-sharing relationships among nonkin vampire bats

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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.

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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.

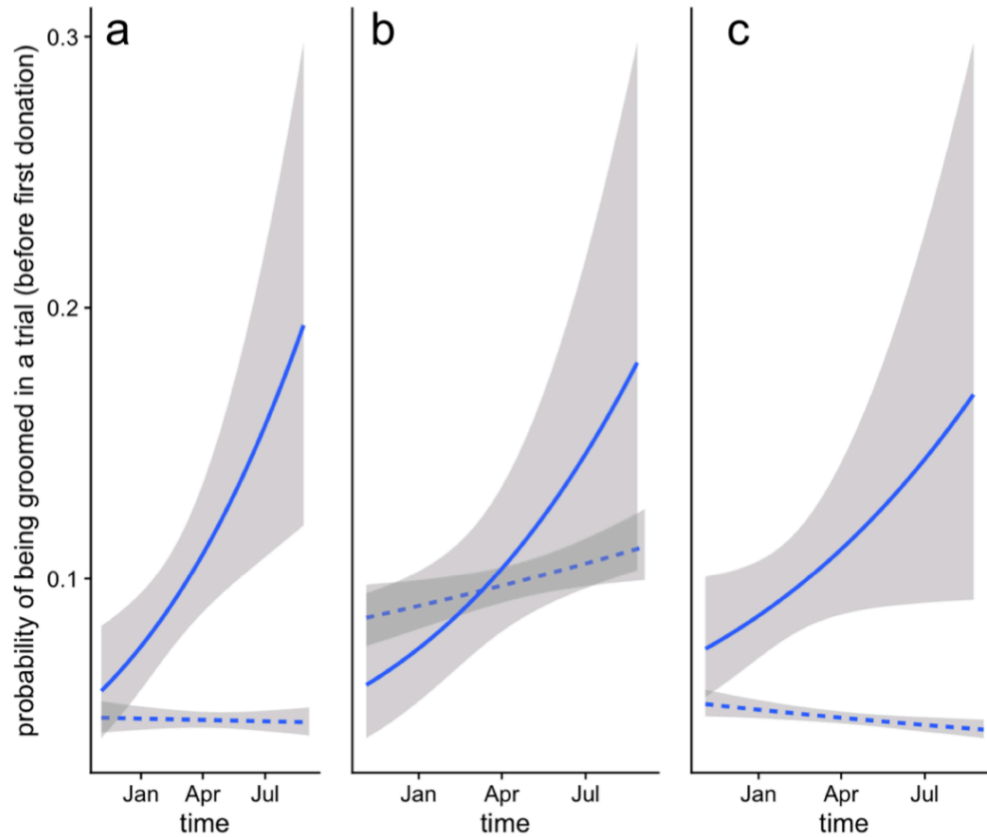
102 To test our hypotheses, we compared the observed coefficients from general and generalized  
103 linear models (slopes  $\beta$ , and odds ratios OR, respectively) to expected distributions of coefficient values  
104 expected under the null hypotheses using permutations of the network or the event 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).

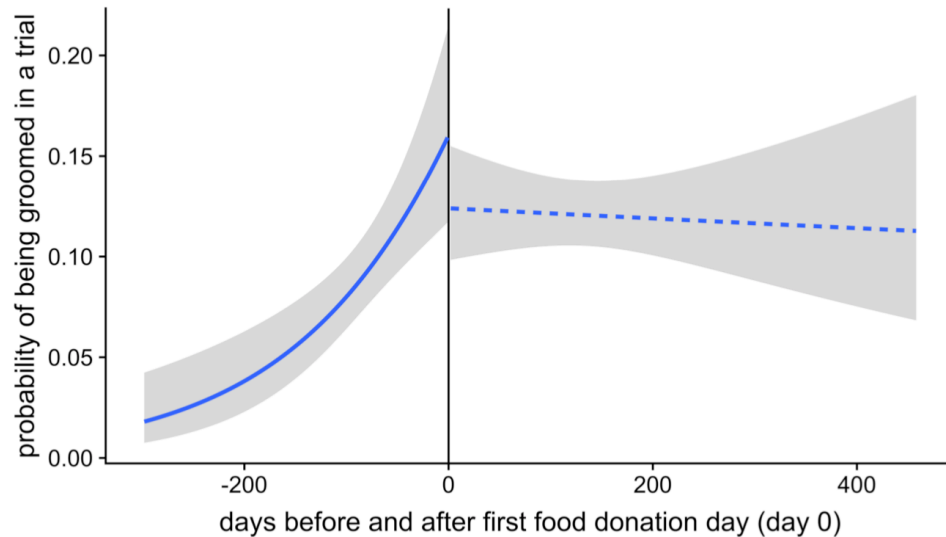
128 If the bats use low-cost grooming to build higher-cost sharing bonds, then the grooming rate  
129 should predict the probability of the first food donation in the opposite direction. As expected, new food  
130 sharing emerged on days after we observed mutual grooming more than expected by chance (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).

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**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

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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

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