

1 **Title**

2 **Evidence for unfamiliar kin recognition in vampire bats**

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16

17 Abstract:

18 Kin discrimination allows organisms to preferentially cooperate with kin, reduce kin  
19 competition, and avoid inbreeding. In vertebrates, kin discrimination often occurs through  
20 prior association. There is less evidence for recognition of unfamiliar kin. Here, we present  
21 the first evidence of unfamiliar kin recognition in bats. We captured female vampire bats  
22 (*Desmodus rotundus*) from a single roost, allowed them to breed in captivity for 22 months,  
23 then released 17 wild-caught females and six captive-born daughters back into the same wild  
24 roost. We then used custom-built proximity sensors to track the free-ranging social  
25 encounters among the previously captive bats and 27 tagged control bats from the same roost.  
26 Using microsatellite-based relatedness estimates, we found that previously captive bats  
27 preferentially associated with related control bats, and that captive-born bats preferentially  
28 associated with unfamiliar kin among control bats. Closer analyses showed that these  
29 unfamiliar-kin-biased associations were not caused by mothers or other familiar close kin,  
30 because the kinship bias was evident even when those bats were not nearby. This striking  
31 evidence for unfamiliar kin recognition in vampire bats warrants further investigation and  
32 provides new hypotheses for how cooperative relationships might be driven synergistically  
33 by both social experience and phenotypic similarity.

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35

36 Keywords: biologging, *Desmodus rotundus*, kin discrimination, kin-biased association,  
37 proximity sensing

38

## 39 **Background**

40 Genetic relatedness plays a pivotal role in the evolution of social behaviour [1, 2]. For  
41 organisms that regularly interact with relatives and non-relatives, kin discrimination allows  
42 for social behaviours that increase inclusive fitness, including helping kin, reducing kin  
43 competition, and avoiding inbreeding. In vertebrates, kin discrimination often occurs through  
44 prior association [3], but there are far fewer reports for the ability to detect unfamiliar kin,  
45 which requires some form of phenotype matching [4]. Experimental evidence for unfamiliar  
46 kin recognition comes from fish [5], amphibians [6, 7], birds [8], rodents [9, 10], and  
47 primates [11, 12].

48 Surprisingly little is known about kin discrimination in bats. Many of the more than  
49 1,400 bat species demonstrate traits linked to the evolution of kin discrimination, including a  
50 low mean and high variance in group kinship [13, 14], budding dispersal [15, 16], preferred  
51 associations [14], and in some cases, nepotistic helping that bestows large fitness benefits  
52 [17]. The clearest example of kin-biased helping in bats is regurgitated food sharing in  
53 vampire bats [17]. Common vampire bats show preferred co-roosting associations with both  
54 kin and nonkin (mean within-roost relatedness = 0.08 [18, 19]). Yearling males disperse  
55 whereas females are typically philopatric and form long-term cooperative relationships within  
56 and between matrilineal groups [17, 20]. Food-sharing in the wild is kin-biased even when controlling  
57 for co-roosting association [17]. However, in all studies to date with this species, cooperating  
58 kin have also been familiar, so it remains unclear whether vampire bats can identify  
59 unfamiliar kin.

60 Here, we show that vampire bats (*Desmodus rotundus*) preferentially associated with  
61 kin that they have been separated from for almost two years, and using captive-born bats, we  
62 also show evidence for unfamiliar kin recognition. We captured female vampire bats from a  
63 wild population, housed them in captivity for 22 months, then attached proximity sensors on

64 17 adult females and six captive-born daughters, and released these 23 ‘test bats’ back into  
65 the roost where they—or their mothers—were originally captured. As a control group, we  
66 also fitted a sample of 27 ‘control bats’ from the same wild population with the same  
67 proximity sensors, which track the time, duration, and signal strength (as a distance estimate)  
68 of all tagged bats within proximity. By genotyping the tagged bats, we were able to test for  
69 kin-biased association between the test bats and the control bats. Surprisingly, the captive-  
70 born bats spent more time near unfamiliar kin in the control group than expected by chance,  
71 even when accounting for the presence of familiar kin. This finding is the first evidence of  
72 unfamiliar kin recognition in a bat.

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## 76 **Methods**

### 77 *Proximity sensing*

78 To track free-ranging associations between the 23 previously captive test bats and 27  
79 control bats, we fitted them with 1.8-g proximity sensors, custom-developed for the BATS  
80 tracking system [21, 22]. The animal-borne sensors sense dyadic proximity among all tagged  
81 individuals that are within communication range (up to five meters), every two seconds.  
82 When two sensors come within communication range, the start of a meeting is logged. When  
83 the sensors go outside this range for 10 or more seconds, the meeting is closed and the on-  
84 board memory stores the meeting start time, duration, maximum received signal strength  
85 indicator (RSSI), and both sensor IDs. All meeting data are remotely downloaded to a base  
86 station, which we placed inside the bat roost during this study [23]. The tagged bats weighed  
87 27-48 g, so tags were 3.8-6.7 % of body mass.

88

89 *Study design*

90 To create the test group, we captured adult females using mist nets outside a hollow  
91 tree in Tolé, Panama on December 13, 2015, then housed them in a captive colony in a 1.7 x  
92 2.1 x 2.3 m outdoor flight cage at the Smithsonian Tropical Research Institute in Gamboa,  
93 Panama, for 22 months [23, 24]. During that time, six female offspring were born into the  
94 captive colony, which were 10-19 months old at the time of our study. The bats in this ‘test  
95 group’ were individually marked with subcutaneous passive integrated transponders and a  
96 visually unique combination of forearm bands.

97 On September 20, 2017, we fitted the 23 test bats with proximity sensors and released  
98 them at the original hollow tree at 2012 h. As a control group, we also captured, banded and  
99 fitted proximity sensors to 27 adult females caught at the same roost and released them back  
100 between 0450 h to 0630 h on September 20. The hollow tree was large enough to contain  
101 distinct social groups, and we estimated the tree to contain about 200 vampire bats based on  
102 captures and photographs. The main cavity was about 1.5 m wide and 2.5 m high, and several  
103 smaller cavities branched off from the main one.

104 To define roosting association rates at a given time period, we summed durations of  
105 meetings with maximum RSSI that correspond to at least 50 cm of proximity, following a  
106 previous analysis [23]. We measured dyadic associations from 0600 h to 2400 h from  
107 September 20-28. We did not include the hours between 0000 h and 0600 h because many  
108 individuals went foraging during this time period. Two control bats and one wild-born test  
109 bat left the study site on the first sampling day. Relatedness data was missing for one control  
110 bat, and one captive-born bat was unrelated to all others in the wild colony. Consequently, the  
111 data underlying the analyses come from 21 test bats (including five captive-born daughters)  
112 and 24 control bats.

113

114 *Genetic relatedness*

115 To measure relatedness, we extracted DNA from a 3-4 mm wing biopsy punch in 80%  
116 or 95% ethanol using a salt–chloroform procedure, then used a LI–COR Biosciences DNA  
117 Analyzer 4300 and the SAGA GT allele scoring software to genotype individuals at 17  
118 polymorphic microsatellite loci (see Table S2 in [23]). Allele frequencies were based on 100  
119 bats from Tolé and nine bats from another site, Las Pavas, Panama. Genotypes were 99.9%  
120 complete. We used the Wang estimator in the R package ‘related’ [25] to obtain an initial  
121 kinship estimate based on relatedness, then we assigned a zero kinship to dyads with negative  
122 relatedness estimates to ensure that any kin-biased associations were not driven by negative  
123 relatedness values. We also assigned a kinship of 0.5 for known mother-offspring dyads or  
124 dyads with relatedness estimates greater than 0.5. We detected no significant differences in  
125 the mean pairwise relatedness between two control bats (mean = 0.077 [95% CI = 0.064 -  
126 0.088], n = 276), and a test and control bat (mean = 0.067 [95% CI = 0.059 - 0.076], n =  
127 552), as would be expected from a random sample of bats captured from the same colony.

128

129 *Data analysis*

130 We first tested for kin-biased associations across all bats and days (see supplement for  
131 methods and results). Next, we tested for kin-biased associations only in test-control bat  
132 dyads. To do this, we calculated the Pearson’s correlation between relatedness and  
133 association rates in test-control dyads separately for each day, and then calculated the mean  
134 daily correlation as the effect size. We compared this effect size to the expected null  
135 distribution of effect sizes generated from network permutations of the bats present in the tree  
136 within each day, following [23]. This permutation procedure controls for the presence or  
137 absence of bats on each day. To estimate a mean effect size and 95% confidence interval (CI)  
138 for each test bat, we bootstrapped (5,000 iterations) the effect size across the possible test-

139 control dyads within each test bat. This allowed us to visualize each bat's contribution to the  
140 overall kin-biased association.

141 To test for evidence of unfamiliar kin recognition, we analysed association rates  
142 between captive-born test bats and control bats that were previously unfamiliar. One  
143 challenge here is that captive-born bats know their mothers (and possibly other familiar kin),  
144 and these familiar kin could in effect 'introduce' or bias the association between a captive-  
145 born bat and an unfamiliar relative in the wild colony. For example, if captive-born bats stay  
146 close to their mothers, and those mothers associate more with related control bats (also  
147 related to her offspring), the result would be the *false* appearance of kin-biased association  
148 between the captive-born test bats and unfamiliar control bats. Therefore, to remove this  
149 possibility, we first looked at whether the unfamiliar kin encounters were initiated by the  
150 mothers of captive-born bats, by plotting the temporal sequence of encounters (hourly  
151 nonzero association rates) for captive-born daughters and their mothers with each control bat.  
152 Next, we conducted a permutation test which removed the effect of mothers. We calculated  
153 hourly association times between a captive-born bat and all possible control bats, and then  
154 removed all hourly association times where the captive-born bat's mother was associated  
155 with the control bat at any time during that same hour. These 'filtered' associations represent  
156 the time each captive-born bat spent with each control bat without the mother nearby. For an  
157 effect size, we summed these hourly association times within each unfamiliar dyad and  
158 calculated their correlation with dyadic kinship. To get a distribution of expected effect sizes  
159 under the null hypothesis, we repeated this same procedure after first randomizing each  
160 captive-born bat's association times across control bats within each hour, while keeping the  
161 mother's associations the same (5,000 randomizations).

162 We then repeated this analysis, but instead of only removing the hours when mothers  
163 were nearby, we removed hours when any familiar close kin of the captive-born bat was

164 nearby (with close kin defined as a relatedness estimate of 0.125 or higher). Both permutation  
165 tests detected the same effect when we conducted an even more conservative test that only  
166 included non-zero association rates in the analysis (i.e. testing the effect of kinship on  
167 encounter duration but not probability).

168

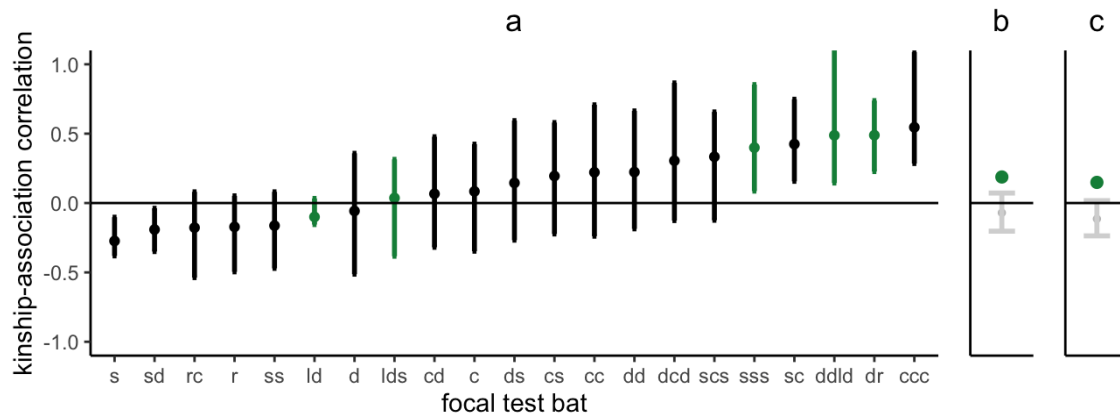
## 169 **Results**

170 We detected a higher-than-chance correlation between genetic relatedness and  
171 association rates (i.e. kin-biased association) across all bats (see supplement). When focusing  
172 only on test-control dyads we also found that association rates between formerly captive test  
173 bats and control bats correlated stronger with genetic relatedness than expected by chance ( $r$   
174 = 0.091,  $p < 0.0002$ ; Figure 1a), and this was true even when excluding captive-born bats ( $r$  =  
175 0.076,  $p < 0.0002$ ). To test for kin-biased association between unfamiliar bats, we limited our  
176 analysis to associations in unfamiliar dyads of a captive-born bat and a control bat in the  
177 absence of familiar kin. Captive-born bats associated with unfamiliar kin more than expected  
178 by chance, even when controlling for the presence of the captive-born bats' mother ( $r = 0.19$ ,  
179  $p = 0.002$ ; Figure 1b) or the presence of other familiar close kin ( $r = 0.15$ ,  $p = 0.0004$ ; Figure  
180 1c).

181

182





183

184 **Figure 1. Kin-biased associations.** Mean correlations between kinship and association with  
185 control bats, shown for each of the 21 test bats (a), were biased above zero. Error bars are  
186 95% CIs from bootstrapping across the 24 control bats. Kin-biased association in captive-  
187 born bats (green) were evident even after removing encounters that involved the captive-born  
188 bat's mother (b) or any familiar kin (c). Larger green dots shown mean correlations across  
189 captive born bats and grey error bars show the 5% and 95% quantiles for the expected mean  
190 correlation to reflect a one-sided test. The timing of kin associations are shown in  
191 supplementary Figures S1-S5. The slopes and values of pairwise kinship and association for  
192 each bat are shown in supplementary Figure S6.

193

## 194 Discussion

195 High-resolution proximity sensing revealed the first evidence of unfamiliar kin  
196 recognition in a bat. When we released captive female vampire bats back into the wild, they  
197 preferentially roosted near closer kin that they were separated from for almost two years.  
198 More importantly, five captive-born daughters with genetic relatives in the control group  
199 preferentially associated with unfamiliar kin, even when the mothers or other familiar close  
200 kin were not present nearby. The chronology of social encounters (Figure S1-5) suggests that  
201 mothers did not initiate most of these encounters. For example, the mother was not nearby in

202 eight of the eleven sampled cases where the captive-born daughter encountered unfamiliar  
203 kin from the control group (relatedness 0.125 or higher) for the first time.

204 Vampire bat social bonds are driven by both kinship and past social experience [17,  
205 23, 24, 26-29]. Both food sharing and association is kin-biased [17], but even when  
206 controlling for kinship, food sharing is reciprocal [24, 26-29] and the previously captive bats  
207 in this study also preferentially associated in the wild with the bats that more frequently  
208 groomed or fed them in captivity [23]. Furthermore, playback studies show that captive  
209 female vampire bats are more attracted to the contact calls of unrelated food donors than to  
210 the contact calls of related groupmates that were non-donors [26]. In this study, we show  
211 evidence that kinship can also drive association without past social experience. The ability to  
212 recognize unfamiliar kin could allow for female bats to preferentially associate or cooperate  
213 with paternal kin or avoid inbreeding with related males.

214 Kinship alone, however, is clearly not sufficient for social integration. Although the  
215 captive-born bats associated more with relatives, they appeared to fail to integrate into the  
216 wild roost [23]. All the captive-born bats left the roost by day six and we did not see them  
217 return. Bites marks on some captive-born bats suggest aggression played a role in their  
218 departure (see [23] for details).

219 Recognizing unfamiliar kin suggests some form of phenotype matching, where  
220 kinship cues (e.g. olfactory [30], visual [11, 12], acoustic [31], or multimodal [32]) are either  
221 learned from familiar kin or matched to one's own phenotype [5]. In vampire bats, both  
222 acoustic and olfaction cues are plausible candidates for unfamiliar kin recognition. Common  
223 vampire bats possess an intact vomeronasal system for detecting pheromones, and have at  
224 least twice as many intact vomeronasal type-1 receptor genes as other sampled bats [33, 34].  
225 Vocal phenotype matching is also plausible given evidence in primates (e.g. [31]) and the  
226 primacy of sound in the social lives of bats [35]. Future work in this species should test

227 whether calls of unfamiliar kin can be discriminated in playback experiments and whether  
228 unfamiliar kin are more likely to develop food-sharing relationships.

229 Our findings relied on extracting signatures of novel behaviours from a large high-  
230 resolution dataset enabled by recent and revolutionary advances in biologging [21], in this  
231 case, miniaturized proximity sensors that log social encounters within largely inaccessible  
232 sites [23, 36]. We suspect that ongoing advances in biologging technology will continue to  
233 reveal many new insights into species that are difficult to directly observe [37-39].

234

### 235 **Ethics**

236 All experiments were approved by the Smithsonian Tropical Research Institute Animal Care  
237 and Use Committee (#2015-0915-2018-A9 and #2017-0102-2020) and by the Panamanian  
238 Ministry of the Environment (#SE/A-76-16 and #SE/AH-2-17).

239

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251

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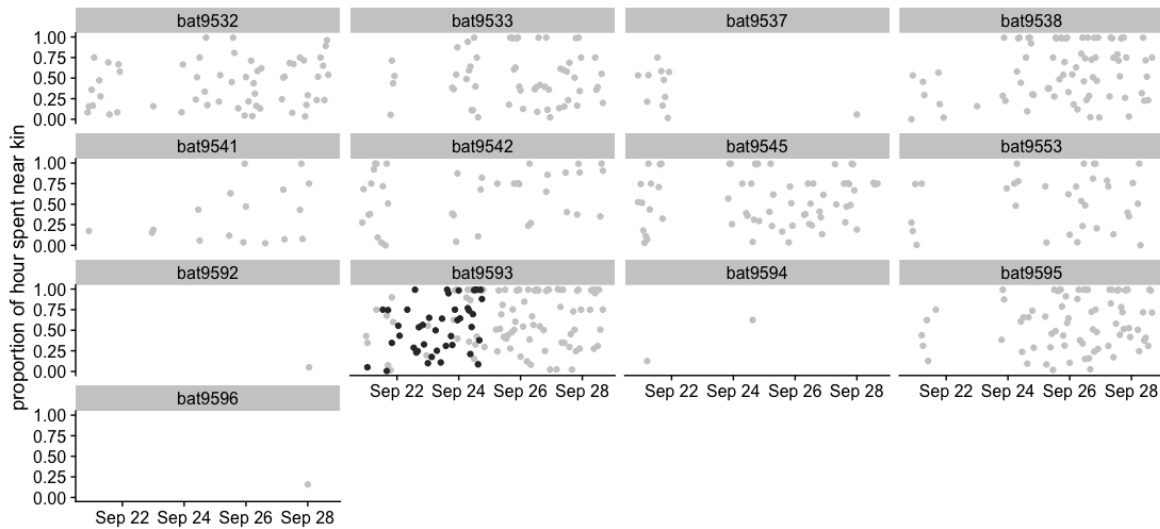
349 **Supplementary Information**

350 **Kin-biased association across all bats**

351 We tested for kin bias in association rates among all test and control bats summed  
352 over the entire study period (including test-test, control-control, and test-control dyads). To  
353 do this, we used the multiple quadratic assignment procedure with double semi-partialling in  
354 the asnipe R package [S1]. This network permutation test allows us to test the effect of  
355 kinship while controlling for a covariate [S2]. Given that test bats preferred to associate with  
356 each other [S3], we controlled for this assortativity by including test-test dyad type as a  
357 covariate (test-test dyads = 1, other dyads = 0) in the first permutation test and including test-  
358 control dyad type (test-control dyads =1, other dyads = 0) in the second permutation test.  
359 Across all bats and days, we detected that more closely related bats were associated longer  
360 than expected by chance (controlling for test-test dyad type: kinship  $\beta = 0.176$ ,  $p < 0.0002$ ;  
361 controlling for test-control dyad type: kinship  $\beta = 0.163$ ,  $p < 0.0002$ ).  
362

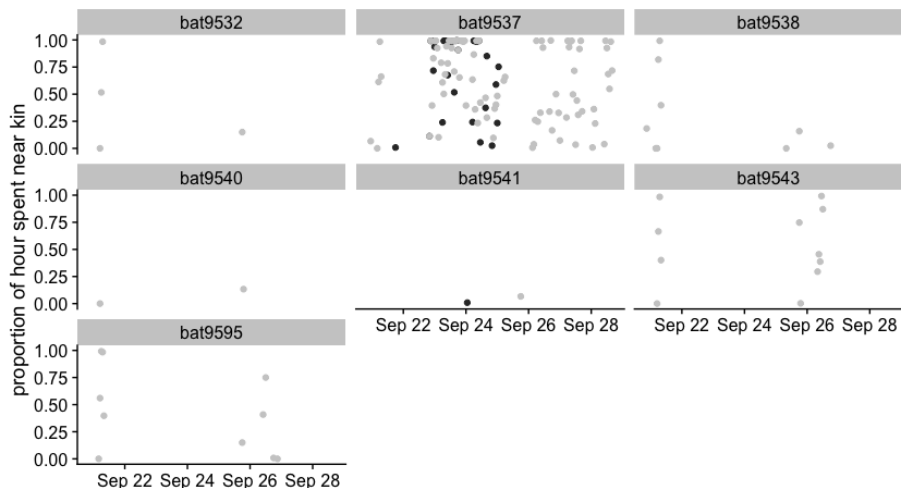


363 **Figures S1-S5: Chronologies of encounters among unfamiliar kin (i.e. captive-born test**  
364 **bats and wild control bats).**



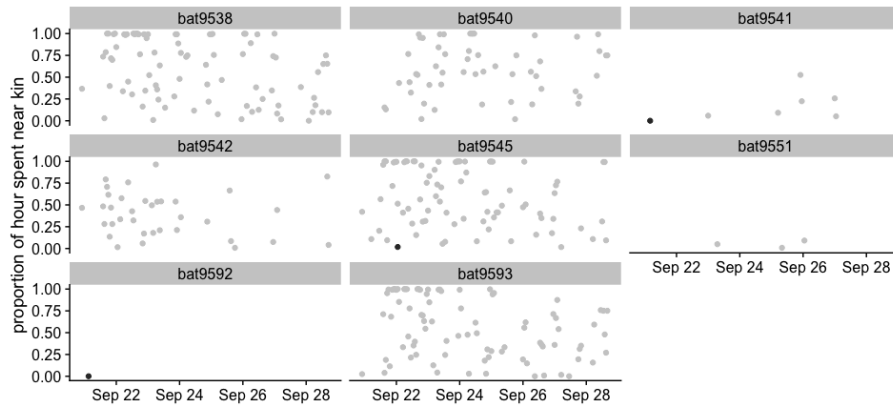
365  
366 Figure S1: Hourly association rates with wild kin (all control bats with genetic relatedness  
367 greater than 0.124 to bat SSS) are shown for bat SSS (captive-born; black dots) and for its  
368 mother (wild-born formerly-captive bat; grey dots).

369  
370

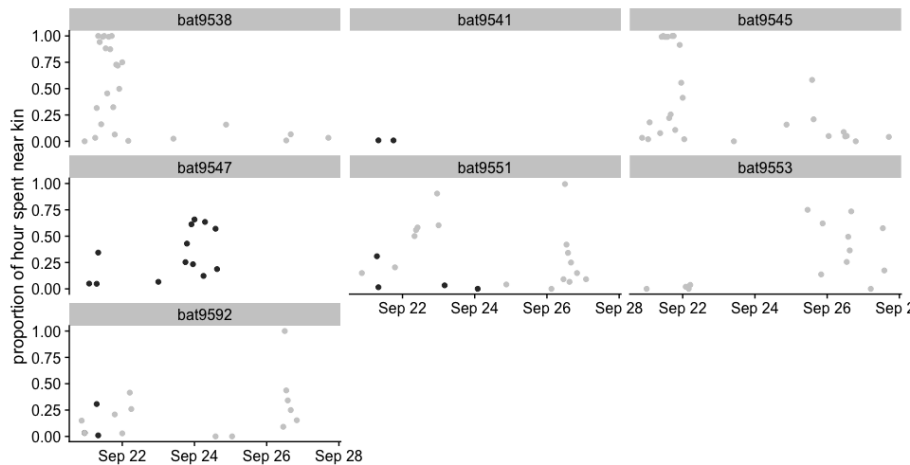


371  
372 Figure S2: Hourly association rates with wild kin (all control bats with genetic relatedness  
373 greater than 0.124 to bat DDL) are shown for bat DDL (captive-born; black dots) and for  
374 its mother (wild-born formerly-captive bat; grey dots).

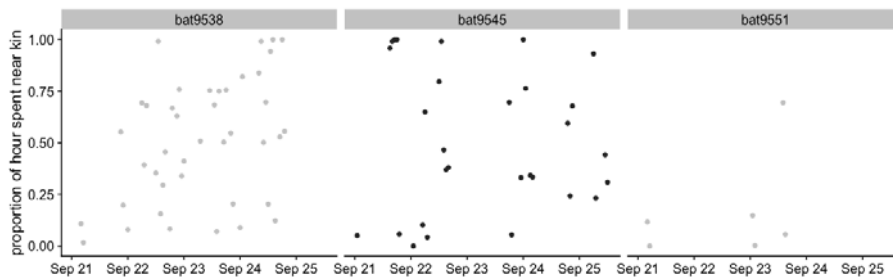
375



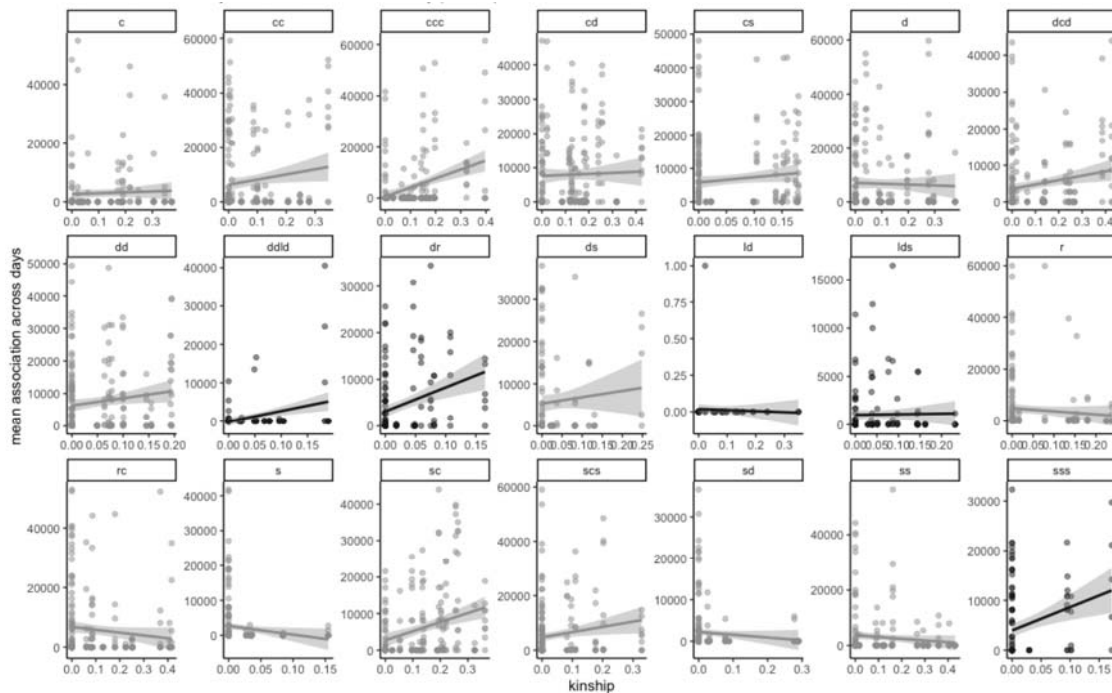
376  
377 Figure S3: Hourly association rates with wild kin (all control bats with genetic relatedness  
378 greater than 0.124 to bat LD) are shown for bat LD (captive-born; black dots) and for its  
379 mother (wild-born formerly-captive bat; grey dots).  
380  
381



382  
383 Figure S4: Hourly association rates with wild kin (all control bats with genetic relatedness  
384 greater than 0.124 to bat LDS) are shown for bat LDS (captive-born; black dots) and for its  
385 mother (wild-born formerly-captive bat; grey dots).  
386  
387



388  
389 Figure S5: Hourly association rates with wild kin (all control bats with genetic relatedness  
390 greater than 0.124 to bat DR) are shown for bat DR (captive-born; black dots) and for its  
391 mother (wild-born formerly-captive bat; grey dots).



392  
393 **S6. Kin-biased associations by bat.** Each panel is a test bat. Each data point ( $n = 3199$ )  
394 represents an association rate (s per sample day) between that test bat and a control bat on a  
395 given sampling day. Points are transparent to show overlapping points. Black slopes are  
396 captive-born test bats and grey slopes are wild-born test bats. Slopes and their 95%  
397 confidence intervals are estimates by treating association rates on different days as  
398 independent (because bats left the tree and returned between sample days).  
399

400

401

#### 402 **References for Supplement:**

403

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