

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36

Social foraging in vampire bats is predicted by long-term cooperative relationships

Simon P. Ripperger^{*,1,2,3}, Gerald G. Carter^{*,1,2}

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

² Smithsonian Tropical Research Institute, Balboa, Ancón, Panamá

³ Museum für Naturkunde, Leibniz-Institute for Evolution and Biodiversity Science, Berlin, Germany

* Corresponding authors: simon.ripperger@gmail.com, carter.1640@osu.edu

Abstract

Stable social bonds in group-living animals can provide greater access to food. A striking example is that female vampire bats often regurgitate blood to socially bonded kin and nonkin that failed in their nightly hunt. Food-sharing relationships form via preferred associations and social grooming within roosts. However, it remains unclear whether these cooperative relationships extend beyond the roost. To evaluate if long-term cooperative relationships in vampire bats play a role in foraging, we tested if foraging encounters measured by proximity sensors could be explained by wild roosting proximity, kinship, or rates of co-feeding, social grooming, and food sharing during 22 months in captivity. We assessed evidence for six hypothetical scenarios of social foraging, ranging from individual to collective hunting. We found that female vampire bats departed their roost individually, but often re-united far outside the roost. Nonrandomly repeating foraging encounters were predicted by within-roost association and histories of cooperation in captivity, even when controlling for kinship. Foraging bats demonstrated both affiliative and competitive interactions and a previously undescribed call type. We suggest that social foraging could have implications for social evolution if 'local' cooperation within the roost and 'global' competition outside the roost enhances fitness interdependence between frequent roostmates.

Short title: Social foraging in vampire bats

37 Introduction

38
39 Socializing and foraging are two key determinants of reproduction and survival that can
40 influence each other in several interesting ways. Preferred social relationships can drive
41 foraging decisions (e.g. great tits: Firth et al. (2015)). Conversely, shared foraging behaviors
42 might shape how relationships form (e.g. bottlenose dolphins: Machado et al. (2019)). Social
43 relationships can determine access to food because closely affiliated individuals can
44 peacefully co-feed at a food patch, hunt together (Lang and Farine, 2017), cooperatively
45 defend food patches (e.g. Emery et al., 2007; Robichaud et al., 1996; Seed et al., 2008), or
46 even give food to less successful foragers (e.g. chimpanzees: Samuni et al. (2018)). Access
47 to food is therefore one benefit of long-term *cooperative relationships*, i.e. stable preferred
48 associations that involve cooperative investments such as grooming and food sharing. For
49 example, grooming in chacma baboons promotes tolerance during foraging (King et al.,
50 2011), and vervet monkeys strategically groom individuals that control access to food due to
51 social dominance (Borgeaud and Bshary, 2015) or an experimentally manipulated ability to
52 access food (Fruteau et al., 2009). A particularly clear non-primate example of cooperative
53 relationships providing food occurs in common vampire bats where females regurgitate
54 ingested blood to socially bonded kin and nonkin that failed to feed that night (Carter and
55 Wilkinson, 2013; Wilkinson, 1984).

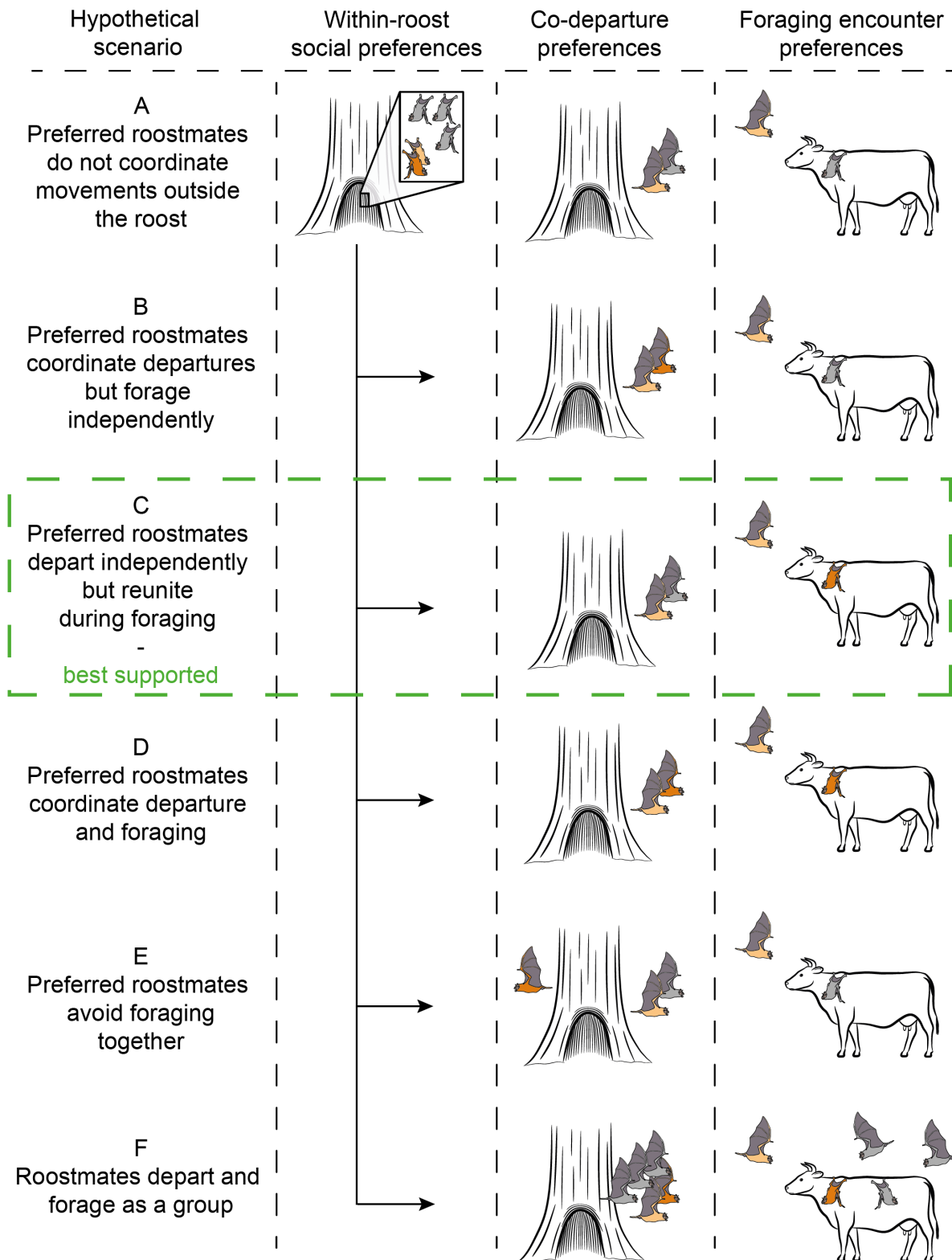
56
57 Food-sharing relationships in vampire bats form as preferred associates escalate social
58 grooming (Carter et al., 2020). These preferred associations and cooperative interactions
59 occur within the day roost. However, little is known about if or how cooperative relationships
60 extend beyond the roost. For example, foraging with socially bonded roostmates might
61 increase efficiency in searching for prey or feeding from wounds, but it remains unclear if or
62 how vampire bats perform social hunting. Several authors provide anecdotal evidence for:
63 groups of females apparently flying together, adult females departing roosts in groups of 2-6,
64 and groups arriving together at a pasture, or approaching and circling prey (Crespo et al.,
65 1974; Greenhall et al., 1971; Wilkinson, 1985; Wilkinson, 1988). There are also observations
66 of up to four individuals feeding simultaneously from different wounds on the same cow
67 (Greenhall et al., 1971), or pairs feeding on the same wound (Greenhall et al., 1971;
68 Wilkinson, 1985). Wilkinson (1985) described evidence that mother-daughter pairs co-forage
69 and share wounds, but found no evidence that frequent roostmates forage together.

70
71 Social foraging can take many forms, from mere aggregations attracted to a common
72 resource to coordinated foraging groups with differentiated roles. Socially-hunting species
73 can be placed on a spectrum of resource sharing from individual foragers competing to
74 group-level sharing (Lang and Farine, 2017). The form of social foraging and the scale of
75 competition over resources outside the roost can have implications for the evolution of food-
76 sharing relationships. Several evolutionary models of vampire bat food sharing as multi-level
77 selection view them as foraging individually then sharing food at the group-level (Di Tosto et
78 al., 2007; Foster, 2004; Witkowski, 2007), but this view contrasts with evidence that food-
79 sharing relationships within groups are reciprocal and highly differentiated (Carter and
80 Wilkinson, 2015; Wilkinson, 1984). An alternative possibility is that individualized
81 relationships drive both within-roost resource sharing and social hunting. This hypothesis is
82 not mutually exclusive with group hunting, because even if individuals forage in groups,
83 specific pairs could be more likely to compete or share a wound or host (Delpietro et al.,
84 2017; Greenhall et al., 1971; Wilkinson, 1985; Wilkinson, 1988).

85
86 Here, we assessed the relative evidence for a range of hypothetical scenarios that vary in
87 degree of coordination of social foraging among socially bonded bats (Figure 1). Preferred
88 roostmates might not coordinate their behavior outside the roost. If instead bats optimize
89 individual foraging efficiency by preferentially depart, follow, or forage with their preferred
90 roostmates, then within-roost networks should predict co-departures or foraging encounters.
91 Alternatively, to maximize their collective search area, bats might prefer to forage with bats
92 outside their network of cooperative relationships and actually avoid foraging with their

93 frequent roostmates. If so, within-roost and outside-roost networks should be negatively
94 correlated. Finally, if entire roosting groups also forage together, then we expect highly
95 correlated within-roost and outside-roost networks.

96
97 To evaluate evidence for these scenarios, we tested whether nightly foraging departures and
98 encounters were predicted by: kinship, roosting associations based on two levels of proximity
99 (during the previous day or over the whole study), and rates of social grooming, food sharing,
100 and co-feeding in captivity. To document roosting associations and foraging encounters, we
101 analyzed social encounter data from proximity sensors placed on 50 free-ranging vampire
102 bats. As additional predictors for 23 of these bats, we used unpublished data on captive co-
103 feeding rates and published long-term rates of social grooming and food sharing (Ripperger
104 et al., 2019). Using simultaneous ultrasonic recording and infrared video, we also describe a
105 distinct new type of vampire bat call only observed during hunting interactions. Our findings
106 illustrate how within-roost cooperative relationships influence foraging in vampire bats and
107 how social networks can vary across contexts.



108
109
110
111
112
113
114
115
116
117

Figure 1. Hypothetical scenarios for how within-roost relationships predict foraging. For the same roosting association networks, each scenario predicts different outcomes for how preferred roosting relationships correlate with co-departures or encounters during foraging. Preferred roostmates (shown as pair of light brown and dark brown bats) might either: not coordinate their behavior outside the roost (A), coordinate only their departures (B), depart independently and then reunite during foraging (C), coordinate departures and foraging (D), or avoid foraging together (E). Alternatively, the bats could depart and forage as a large group (F).

118 **Methods**

119

120 **Subjects**

121 Subjects were common vampire bats (*Desmodus rotundus*) including 27 wild-caught adult
122 females that were tagged and released, and 23 previously captive females (17 adults and
123 their six subadult captive-born daughters) that had spent the past 22 months in captivity and
124 were then tagged and released back into their wild roost tree (see Carter et al., 2020;
125 Ripperger et al., 2019). See supplement for details.

126

127 **Kinship**

128 We assumed that known mother-daughter pairs had a kinship of 0.5. To estimate kinship for
129 all other pairs, we genotyped bats at 17 polymorphic microsatellite loci (DNA isolated via a
130 salt-chloroform procedure from 3-4 mm biopsy punch stored in 80 or 95% ethanol), then
131 used the Wang estimator in the R package 'related'. See supplement for details.

132

133 **Past cooperative interaction rates in previously captive bats**

134 To measure cooperative relationships in the previously captive bats, we used previously
135 published rates of social grooming and food sharing from experimental fasting trials (Carter
136 et al., 2020). See supplement for details. To assess tolerance while feeding, we also
137 analysed previously unpublished data on co-feeding among the same captive vampire bats.
138 Social interactions were observed at blood spout feeders while the bats were in captivity,
139 including 1300 competitive interactions and 277 cases of co-feeding where two bats were
140 observed feeding from the same blood spout at the same time (from 1050 h of observation
141 from 70 nights). We used 201 co-feeding events with identified bats to construct a co-feeding
142 network of the number of dyadic co-feeding events (range = 0 to 6) for each pair.

143

144 To assess correlations between the captive co-feeding network and networks of food sharing
145 or social grooming, we used Mantel tests. To test the same correlation while controlling for
146 overlap in individual feeding times, we also used a custom double permutation test (Farine
147 and Carter, 2020). This procedure calculates an adjusted co-feeding rate for each pair as the
148 difference between the observed co-feeding rate and the median expected co-feeding rate
149 from 5000 permutations of the co-feeding bat identities, permuted among the bats seen
150 within each hour. The results of this constrained permutation test and the unconstrained
151 Mantel test were similar and gave the same conclusion, so we report only the results from
152 the double permutation test. To test for preferred captive co-feeding partners, we also used
153 the same within-hour permutations to test if social differentiation in co-feeding (the coefficient
154 of variation in co-feeding rates) was greater than expected from the null model.

155

156 **Association rates in the wild using proximity sensors**

157 We placed custom-made proximity sensors on all 50 female common vampire bats (sensor
158 mass: 1.8 g; 4.5-6.9 % of each bat's mass) that automatically documented dyadic
159 associations among all 50 tagged bats when those come within reception range (max. 5-10
160 m). To log encounters, each proximity sensor broadcasted a signal every two seconds to
161 update the duration of each encounter. We used 1 s as the duration of encounters that were
162 shorter than two successive signals (i.e., encounters shorter than two seconds). The
163 maximum signal strength of each encounter can be used as an estimate for a minimum
164 proximity between two tagged bats during the encounter by comparing the signal intensity to
165 a calibration curve (Ripperger et al., 2019; Ripperger et al., 2020b).

166

167 We collected association data on the free-ranging bats at Tolé, Panama (8°12'03"N
168 81°43'46"W), a rural area that is mainly composed of cattle pastures for meat production.
169 Around 200-250 common vampire bats roosted inside a hollow tree on a cattle pasture that
170 was about 15 ha in size. To create a stable food patch, we corralled ca. 100 heads of cattle
171 at a distance of ca. 300 m from the roost from 6pm until 6am between the evening of
172 September 21 until the morning of September 26, 2017 (days 1 to 5 in our study). Before and

173 after that time period, the cattle were ranging freely. A neighboring, much larger pasture west
174 of the roost had about 1,500 heads of cattle within a distance of 1-2 km (Figure S1).

175

176 To construct networks of roosting association rates during each daytime period within the
177 roost, we relied on roosting association data that had been used in a previous study
178 (Ripperger et al., 2019). Based on the same two thresholds of signal strength as before, we
179 defined two categories of proximity: “associations” (within a maximum of ca. 50 cm) and
180 “close contacts” (within ca. 2 cm). Roosting network edges were rates of within-roost
181 association or close contact, i.e. the total time two bats spent in association per unit of time.
182 See supplement for details.

183

184 To log presence and co-occurrence of foraging bats at points outside the roost during the
185 night, we placed base stations (which can detect tagged bats at distances of about 150 m) at
186 the roost and at 5 other locations in the surrounding cattle pastures. To identify departures
187 from the roost, we found the points in time where each bat lost connection from the roost
188 base station and almost all of the many tagged bats in the colony within communication
189 range (i.e., a sudden drop in associations from many bats down to 0-3 bats; see figure 2 in
190 Ripperger et al. (2020b)). Departing bats may have also contacted base stations on the cattle
191 pasture (Figure S1). We used the same kind of data to find the return times to the roost for
192 each bat and night.

193

194 Of the 629 dyadic encounters that occurred one minute after leaving the roost and one
195 minute before arriving at the roost, we excluded 43 encounters from further analysis,
196 because a proximity sensor contacted the roost base station, suggesting that those
197 encounters occurred while bats were roosting at the entrance or on the outside of the roost
198 tree. The remaining 586 encounters occurred farther away, outside the communication range
199 of the roost base station, and we refer to these as “foraging encounters”.

200

201 ***Observing interactions of foraging vampire bats***

202 At Tolé, we only observed two occasions, where two bats stopped at the cattle pasture and
203 were associated (for 3.5 and 4.6 minutes). When releasing the corralled cattle in the
204 morning we observed bite marks but to avoid changing their behavior, we did not get close
205 enough to the cattle at night to record audio or video of bats interacting. To collect direct
206 observations on foraging behavior, we recorded simultaneous audio and video of bat
207 foraging behavior at a different farm near La Chorrera, Panama (8°52'42"N 79°52'05"W)
208 using an infrared (IR) spotlight, IR-sensitive video camera (Sony AX53 4K camcorder) and a
209 Avisoft condenser microphone (CM16, frequency range 1 to 200 kHz) and digitizer (Avisoft
210 USG 116Hbm, 1000 kHz sampling rate, 16-bit resolution) connected to a notebook
211 computer. One observer (SPR) moved with a herd of about 20 grazing cattle without visual
212 light and observed the moving cattle through the viewfinder of the IR camera. To compare
213 social calls made during foraging with calls from inside a roost, we used the same recording
214 equipment to record social calls from a roost only a few hundred meters from the foraging
215 site.

216

217 ***Acoustic analysis of calls in foraging bats***

218 We used Avisoft SASLab Pro (R. Specht, Avisoft Bioacoustics, Glienicke/Nordbahn,
219 Germany; version 5.2.13) to measure acoustic parameters of the social call types. Start and
220 end of calls were determined manually, based on the oscillogram. Subsequent, five acoustic
221 parameters were measured automatically; one temporal (duration) and four spectral
222 parameters (peak frequency at maximum amplitude, minimum and maximum frequency, and
223 bandwidth). Acoustic parameter extraction was restricted to the fundamental frequency.
224 Spectrograms were created using a Hamming window with 1024-point fast Fourier transform
225 and 93.75 % overlap (resulting in a 977 Hz frequency resolution and a time resolution of
226 0.064 ms). To estimate the frequency curvatures of the different call types, we measured the
227 spectral parameters at 11 different locations distributed evenly over the fundamental
228 frequency of each call. To compare call structure from different contexts (roosting vs

229 foraging, antagonistic vs affiliative behavior) in multivariate space, we plotted the first two
230 principal components after entering these measures into a principal component analyses
231 with varimax rotation (using the 'foreign' package in R).

232

233 ***Statistical analysis of foraging behavior***

234 For every bat, we calculated the times over 9 days when it was clearly distant from the roost
235 tree (ESM File 2). To test whether the previously captive bats and never-captive control bats
236 differed in the departure time and duration of their foraging bouts, we fit linear mixed-effect
237 models (LMMs) with type of bats and day as fixed effects and bat as a random effect (p-
238 values estimated with Satterthwaite's degrees of freedom method using the R package
239 lmerTest). To compare consistency of onsets and durations, we measure the unadjusted
240 repeatability (ICC or intra-class correlation) for each type of bat. To see how often tagged
241 bats departed together, we inspected cases where departure times were within one minute.

242

243 ***Preferred associations during foraging***

244 To test if repeated foraging encounters occurred among the same bats more than expected
245 by chance, we used a custom data permutation test that compared observed and expected
246 social differentiation (the coefficient of variation in co-foraging rates, which increases when
247 some pairs have more repeated encounters) while controlling for overlap in foraging times.
248 Since all bats were sampled evenly within each night and most foraging encounters were
249 brief (median = 1 second), we first used a simple and conservative measure of co-foraging
250 rates based on counting the presence or absence of an encounter during each hour outside
251 the roost over 9 days (counts varied from 0 to 15). For instance, if two bats met twice in the
252 same hour bin, this is still one encounter. These binary observations could be swapped in
253 our null model. To generate a null distribution of 5000 social differentiations expected by
254 chance, we permuted one bat in every dyad to a random possible partner that was also
255 present outside the roost in that same day and hour (to control for overlaps in foraging
256 times).

257

258 ***Predictors of social foraging***

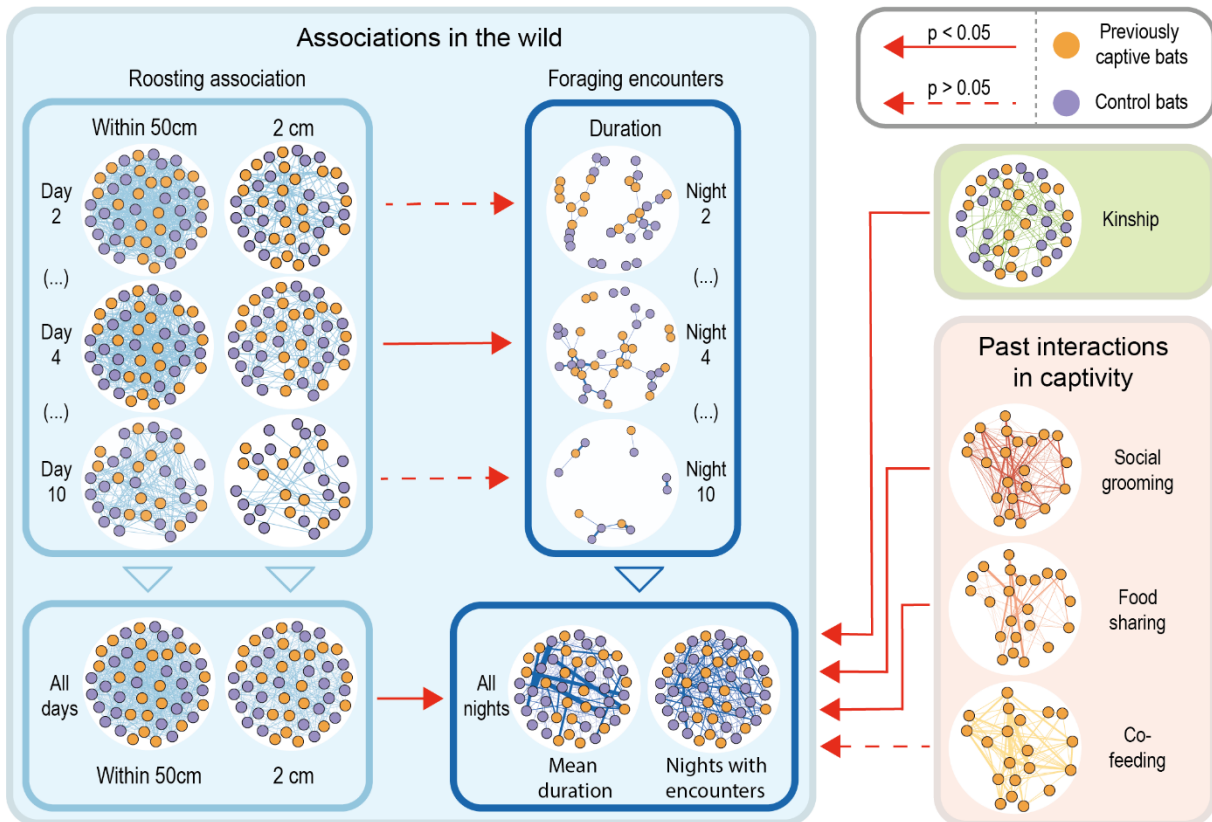
259 To test predictors of social foraging, we constructed foraging encounter networks where
260 edges were based on either duration of total encounter time outside the roost (seconds) or
261 number of days with foraging encounters (0-9). The latter response variable is far more
262 conservative because it only counts repeats across different days. We included the following
263 predictors: kinship, two proximity levels of within-roost association, social-grooming rate,
264 food-sharing rate. We also tested the effect of dyad type (i.e. both bats previously captive,
265 both bats never captive, one bat previously captive, and both bats captive-born juveniles).
266 We did not use number of nights with foraging encounters as a response for tests that only
267 included the previously captive bats, because 9 of them (including all captive-born bats) left
268 the roost during the study period (Ripperger et al., 2019). To measure how much longer
269 foraging encounters were between kin versus nonkin, we fit a linear mixed effects model with
270 log-transformed duration as the response variable, kinship greater than 0.1 as a binary fixed
271 effect, and both bats' identities as random effects, then converted model coefficients into a
272 percentage difference.

273

274 To test the effect of predictor networks on a response network, we used regression quadratic
275 assignment procedure (QAP) for single predictors, or multiple regression quadratic
276 assignment procedure with double semi-partialling (MRQAP) for two predictors (using the
277 'asnipe' R package (Farine, 2013)). To create null models, we used constrained (within-day)
278 node-label permutations. This approach is necessary for preserving the daily and nightly
279 network structure (e.g. distribution of edges and edge weights) and for controlling for the
280 presence or absence of bats in the roost each day. To control for foraging bout overlap in
281 each pair, we included that measure as a covariate. We also used QAP to test whether the
282 within-roosting association on each day, predicted the subsequent foraging network that
283 night. We then bootstrapped the mean of the slopes across the eight days to test for an
284 overall paired day-night effect.

285 **Consistency of individual social traits**

286 To test whether bats that are more socially connected within the roost are also more
287 connected in foraging networks, we tested if the nodes' degree centrality was correlated
288 between roosting and foraging networks. We measured degree centrality independently
289 within each day or night network when the bat was present and then took the mean for each
290 bat. Bats with no encounters in that day or night were considered missing for that day (i.e.
291 not counted as zero degree). We fit general linear mixed effect models with foraging network
292 centrality as the response variable, roosting network centrality (either association and close
293 contact) as fixed effect, and bat as random effect. P-values were calculated from 5000
294 permutations of the bat's foraging centralities within each night. These constrained node-
295 label permutations (within night) are necessary to control for the fact that foraging and
296 roosting network centralities could be correlated simply by some bats being present at the
297 site longer.
298



299 **Figure 2: Network comparisons.** Foraging encounter rates were predicted by roosting
300 associations, kinship, and previous long-term rates of social grooming and food sharing in
301 captivity. To facilitate visual comparisons, we fixed the spatial coordinates of each node
302 (except for the sparse night-by-night foraging networks), we scaled edge strength in each
303 network, and we removed nodes without edges. In the kinship network, only edges with
304 kinship estimates > 0.24 are shown and bats without kin in the group are not shown. In the
305 paired night-day networks of association in the wild, we only detected a clear correlation
306 between day and night on day 4 (Table S1).
307
308

309 Results

310

311 ***Sampled bats did not depart together***

312 The never-captive control bats departed from the roost 8.3 hours after sunset and returned
313 2.5 h later, on average (ESM 2). The previously captive bats foraged earlier and less
314 predictably (see below). We observed only five cases where two bats departed within five
315 seconds of each other and none of these cases was followed by a foraging encounter. For
316 the cases where pairs did have a foraging encounter, the shortest differences in departure
317 times were 8, 21, and 28 s.

318

319 ***Previous captivity influenced departures and foraging***

320 Compared to the wild control bats, the previously captive bats departed the roost on average
321 1.6 hours earlier ($t = -4.55$, $p < 0.0001$), but they did not forage consistently longer (LMM;
322 $t = 1.29$, $p = 0.2$, ESM 2). The captive-born bats departed 2 hours earlier ($t = -3.15$, $p = 0.002$)
323 and also did not forage longer ($t = -0.41$, $df = 47.8$, $p = 0.7$) than control bats. All these
324 models control for departure times being on average 14 minutes later each day ($t = 6.6$, $p <$
325 0.0001 , ESM 2), perhaps due to moonset times being 20-40 min later each day during the
326 study period. The total duration of foraging encounters did not clearly differ between types of
327 pairs (Figure S3A), but pairs of control bats had significantly more nights with foraging
328 encounters (Figure S3B) compared to other types of pairs, possibly due to control bats
329 having more consistent foraging times. Departure times were more consistent across days
330 within each control bat (intraclass correlation coefficient (ICC) = 0.58) compared to within
331 each previously captive bat (ICC = 0.21) or captive-born bat (ICC = 0). The duration of the
332 longest foraging bout was also more consistent in wild control bats (ICC = 0.54) than the
333 previously captive bats (ICC = 0.35) or captive-born bats (ICC = 0.15).

334

335 ***Preferred associations in foraging encounter networks***

336 Foraging encounters were orders of magnitude shorter in duration than within-roost
337 encounters, their median duration was 1 s, and they never exceeded 30 minutes (ESM 1,
338 Figure S2). Of 151 pairs with a foraging encounter, 45 did this repeatedly across 9 nights.
339 The variation in number of hours in which two bats reunited was greater than expected from
340 our null model that simulated random encounters among bats that were outside the roost in
341 the same hour (observed coefficient of variation = 4.36; $p < 0.001$; 95% of expected values: -
342 2.2 to 2.4). Most of these foraging encounters occurred at locations outside our sampled
343 areas, but 10 (among eight pairs) occurred near the other base stations on the surrounding
344 cattle pastures (ESM 1, Figure S1), and only three foraging encounters (among three pairs)
345 occurred at the corral that we created as a stable food patch about 300 m from the roost (two
346 encounters on days one and three while the cattle were present and one encounter on day
347 seven).

348

349 ***Kinship predicts foraging encounters***

350 Kinship predicted the number of nights with foraging encounters (QAP, $\beta = 15.4$, $n = 46$ bats,
351 $p < 0.0001$) and foraging encounter time ($\beta = 15.4$, $n = 47$ bats, $p = 0.022$) even when
352 controlling for bout overlap (MRQAP, $\beta = 0.10$, $p = 0.002$). The median duration of a foraging
353 encounter for close kin ($r > 0.1$) was 9 s, which was 135% longer in duration relative to the
354 duration of foraging encounters between nonkin ($r < 0.1$; median duration = 1s; $\beta = 0.85$,
355 $df = 175$, $p = 0.001$).

356

357 ***Within-roost association rates predicted foraging encounters***

358 Bats that spent more time near each other within the tree during the day, also spent more
359 time together outside the roost during the night (associations: QAP, $\beta = 29.5$, $p < 0.001$;
360 close-contact: QAP, $\beta = 24.7$, $p = 0.002$) even when controlling for the foraging bout overlap
361 (associations: MRQAP, $\beta = 0.092$, $p = 0.003$; close-contact associations: MRQAP, $\beta = 0.078$,
362 $p = 0.015$). Within-roost associations also predicted a greater number of nights with foraging
363 encounters (associations: QAP, $\beta = 0.07$, $p < 0.001$; close-contact association: QAP, $\beta =$
364 0.04 , $p = 0.021$). The relationship between the within-roost association network and the

365 corresponding night's foraging network was clear within only one of the 8 days (Table S1),
366 but the paired relationships between day and night networks tended to be greater than zero
367 overall (associations: mean $\beta = 0.026$, 95% CI = 0.004 to 0.051; close-contact associations:
368 mean $\beta = 0.018$, 95% CI = 0.003 to 0.04).

369

370 ***Roosting degree centrality predicted foraging degree centrality***

371 Bats that were connected to more associates in within-roost association networks also
372 tended to have more associates in the nightly foraging networks (associations: $\beta = 0.034$, $n =$
373 48 bats, one-tailed $p = 0.008$; close-contact: $\beta = 0.055$, one-tailed $p = 0.078$; Figure S4).

374

375 ***Cooperative relationships in captivity predict foraging encounters in the field***

376 In the previously captive bats, foraging encounter time was predicted by social grooming
377 (QAP, $\beta = 26.5$, $n = 22$, $p = 0.032$; MRQAP controlling for bout overlap: $\beta = 0.12$, $p = 0.063$)
378 and food sharing ($\beta = 38.7$, $n = 22$, $p = 0.015$; MRQAP controlling for bout overlap: $\beta = 0.20$,
379 $p = 0.014$), and food sharing when controlling for kinship (MRQAP, sharing: $\beta = 0.16$, $p =$
380 0.022; kinship: $\beta = 0.14$, $p = 0.049$). Kinship and cooperative relationship were therefore
381 independent predictors of social foraging.

382

383 ***Co-feeding among familiar captive bats was not limited to cooperative relationships.***

384 In contrast to the measures of social foraging in the field, we detected only weak evidence for
385 preferred associations during co-feeding in captivity (social differentiation = 2.10, $p = 0.047$
386 when controlling for hour, $p = 0.041$ when not controlling for hour), and we found no
387 correlation between captive co-feeding and social grooming ($r=0.008$, $p=0.36$), food sharing
388 ($r=0.015$, $p=0.28$) or social foraging time in the wild ($r=0.003$, $n=20$, $p=0.42$).

389

390 ***Behavioral interactions during foraging***

391 To record a sample of bat interactions during foraging encounters, we recorded infrared
392 video and ultrasonic audio of 14 interactions between foraging vampire bats (Tables S2 and
393 S3). Social calls during foraging had three general spectral shapes (Figures S5 and S6):
394 "downward sweeping calls" have been recorded often in roosts and are produced by socially
395 isolated vampire bats in captivity (Carter et al., 2012; Carter and Wilkinson, 2016). "Buzz
396 calls" were noisy without clear tonal structure and occurred during antagonistic interactions.
397 We observed "n-shaped calls" produced by bats interacting while near cattle (Figure S6), and
398 to our knowledge this call type has never been seen in wild roosts, from confrontations at the
399 feeders in captivity (Sailler and Schmidt, 1978), or from individually isolated bats in captivity
400 (Carter et al., 2012, Carter, unpublished data).

401

402

403 **Discussion**

404

405 ***Long-term cooperative relationships predicted repeated foraging encounters***

406 Tagged female vampire bats departed the roost individually, but often re-united far from the
407 roost during foraging bouts. The rates of these foraging encounters were consistently higher
408 than expected in specific pairs and predicted by roosting associations, kinship, and by the
409 history of social grooming and food sharing in captivity, even when controlling kinship.

410 Previous experiments with female vampire bats suggest that these measures—roosting
411 proximity, social grooming, and food sharing—reflect an underlying cooperative relationship
412 (Carter et al., 2020; Carter and Wilkinson, 2013; Ripperger et al., 2019; Wilkinson, 1984;
413 Wilkinson, 1985). In this study, we knew the cooperation histories among the previously
414 captive bats, and that these individuals had no interactions with the control bats for at least
415 the previous 22 months. We could therefore infer that relationships that are typically defined
416 by associations and cooperative interactions within roosts, also extend beyond the roost and
417 may provide benefits during foraging. In addition to consistent social relationships across
418 context (from captivity to roosting to foraging), we found that bats that encountered more
419 associates in the roost during the days also encountered more associates while foraging
420 during the nights, suggesting consistent individual variation in social traits.

421 Although some foraging encounters may have occurred before or after foraging, most of
422 these encounters were likely to have occurred during foraging for several reasons. First,
423 foraging encounters were brief, whereas associations among non-moving bats should be
424 much longer in duration (Figure S2). Second, foraging is likely to take up a substantial
425 amount of the limited time outside the roost (mean = 2.4 h). After commuting, searching, and
426 selecting a host, a vampire bat can take up to 30 minutes to select a wound site, 10-40
427 minutes to prepare the wound site, and 9-40 minutes to feed (Greenhall, 1972; Greenhall et
428 al., 1971). Third, we used infrared video to observe several interactions on or near cattle that
429 were consistent with the short durations of foraging encounters in the proximity data (e.g.,
430 Videos S1, S2, S4). Fourth, foraging encounters among close female kin had a median
431 duration of 9 s and were longer than among non-kin (median duration of 1s), which is
432 consistent with observations that affiliative interactions last longer.

433

434 ***No clear evidence for highly coordinated collective movements***

435 For animals with fluid social structures (e.g. high fission-fusion dynamics), it is important to
436 clarify the ambiguous meaning of a “social group”, and similarly, one must distinguish
437 between different possible forms of “social foraging” (Lang and Farine, 2017). In bats, the
438 relative degree of social coordination during foraging can be difficult to assess and compare
439 due to differing limitations in the observational methods and the lack of knowledge of
440 differentiated social relationships within the colony. In this study, we took advantage of well
441 described within-roost relationships to assess evidence for several alternative scenarios of
442 foraging behavior (Figure 1). Kinship and rates of association and cooperation led to longer
443 and more frequent foraging encounters, but we did not observe highly coordinated joint
444 departures or collective movements (Figure 1). This fluid pattern, of not moving in
445 coordinated stable groups yet repeatedly encountering preferred associates during foraging,
446 is also reflected in co-roosting networks where individuals form roosting groups that
447 frequently change composition, yet maintain preferred relationships over time (Wilkinson,
448 1985). Given the many unsampled bats inside the same tree (~200), it is possible that bats
449 departed with other unobserved roostmates, but we did not see departures of large groups
450 (while catching bats outside the roost) nor did we see evidence for coordination between
451 roosting and departing in the tagged bats.

452

453 The ways that specific bats reunited with preferred associates therefore remains unknown,
454 but the downward sweeping calls that we recorded in foraging bats (Figure S6), are similar to
455 contact calls that captive vampire bats can use to find and recognize preferred partners
456 (Carter and Wilkinson, 2016). The role of calls, in particular a possibly foraging-specific call
457 type (“n-shaped call” Figure S6, Figure S7), warrants further investigation. In several other
458 bat species, there is abundant evidence for socially influenced foraging based on
459 eavesdropping on echolocation calls (e.g. Cvikel et al., 2015; Dechmann et al., 2009;
460 Dechmann et al., 2010; Egert-Berg et al., 2018; Lewanzik et al., 2019). Greater spear-nosed
461 bats in Trinidad appeared to coordinate group foraging based on a group-specific contact call
462 (Wilkinson and Boughman, 1998). Observations of the fish-eating greater bulldog bat
463 suggested that female roostmates depart individually, then assembled into small groups
464 outside the roost to forage together, possibly coordinating their movements with calls
465 (Brooke 1997).

466

467 ***Affiliative and competitive interactions***

468 Given the difficulty of making a bite compared to the ease of drinking from an open wound,
469 some individual vampire bats appear to exploit the bites already made by others, and fights
470 can occur over open wounds or hosts (Delpietro et al., 2017; Greenhall et al., 1971; Sazima,
471 1978; Schmidt, 1978; Wilkinson, 1985), but it remains unclear how often these competitive
472 interactions occur among familiar versus unfamiliar vampire bats. In our study, we observed
473 foraging vampire bats engaging in both affiliative and competitive interactions (see Table S3,
474 Videos S1-5). The competitive interactions were far more aggressive than what we observed
475 among familiar captive bats feeding from an accessible and unlimited source of blood. This

476 observation and our results above are consistent with the hypothesis that competitive
477 interactions are more likely between less familiar bats.

478

479 ***Implications for social dominance***

480 The fluid nature of foraging encounters has potential implications for social dominance.
481 Dominance hierarchies should be common when animals move together in groups, because
482 the same frequent groupmates will also be primary competitors for first access to food.
483 Dominance hierarchies among familiar female vampire bats, which do not always travel or
484 forage together, are indeed less clear and linear than among female mammals that do travel
485 and forage in more stable groups (Crisp et al. unpublished data). Furthermore, blood from an
486 open wound is often not a limited resource, so competition over food might be relatively low
487 among familiar vampire bats that tolerate each other (as observed in captivity) and even
488 share food, compared to unfamiliar conspecifics that might “steal” a wound.

489

490 ***Implications for the evolution of cooperative relationships***

491 Vampire bats might also benefit from foraging with socially tolerant partners by acquiring
492 information on where to feed or by gaining access to open wounds. A single open wound can
493 sequentially feed several bats, and leading a cooperation partner to an open wound on the
494 same host would presumably be less costly to a successful forager than regurgitating blood
495 to that individual later at the roost. Put differently, socially bonded bats would benefit from
496 each other’s foraging success, i.e. interdependence (Roberts, 2005). As seen in ravens, the
497 presence of a socially bonded partner might even allow for joint defense of food against third-
498 parties (Sierro et al., 2020; Szpl et al., 2015).

499

500 Such forms of social foraging in vampire bats may have implications for the spatial scale of
501 competition—a key factor shaping social evolution in humans (West et al., 2006) and other
502 group-living animals (Radford et al., 2016). In female vampire bats, cooperation occurs
503 ‘locally’ with specific frequent roostmates, and competition over food might occur more
504 ‘globally’ with members of the much larger population. If so, a more ‘global’ scale of
505 competition could reduce conflict and increase interdependence among highly associated
506 females. To test this idea, it would thus be useful to determine if sampled groups of vampire
507 bats consistently feed on the same or different prey individuals, and if vampire bats are more
508 likely to approach or avoid the social calls of foraging bats that are frequent roostmates
509 versus unfamiliar conspecifics.

510

511 ***Implications for describing social structure***

512 A major advantage of proximity sensors was the ability to continuously track associations
513 among multiple individual bats both inside and outside their roost, which allows for the
514 construction of dynamic and multi-layer networks. Studies on social foraging and other social
515 behaviors in bats and other small highly mobile vertebrates have historically been limited by
516 the available tracking technology (Ripperger et al., 2020b). Radiotelemetry has poor spatial
517 resolution and continuously tracking many individuals is difficult. Current GPS-tags for bats
518 have rather short runtimes and the tags need to be recovered to download the data. On-
519 board ultrasound recorders (e.g. Egert-Berg et al., 2018) do not reveal the identity of
520 encountered individuals. A major downside to proximity sensors was that many foraging
521 encounters occurred at unknown locations. However, placing proximity sensors or antennas
522 at more locations and on livestock would allow a better reconstruction of foraging behavior. A
523 combination of biologging approaches can also help to overcome existing challenges (e.g.
524 Leoni et al., 2020; Ripperger et al., 2020a). Standardized high-throughput methods for
525 measuring social network structure across bats and other diverse groups allow for
526 comparative studies that assess the relative ecological and evolutionary drivers of social
527 traits and social complexity across species.

528

529 **Acknowledgements**

530

531 Work by S. Ripperger and G. Carter is supported by a grant from the National Science
532 Foundation (Integrative Organismal Systems #2015928). We thank R. Page and F. Mayer for
533 providing funds for this study, which was funded by grants from the Deutsche
534 Forschungsgemeinschaft (DFG) within the research unit FOR-1508, a Smithsonian Scholarly
535 Studies Awards grant, and a National Geographic Society Research Grant WW-057R-17.
536 We thank O. Castrellón and C. de León for permission to conduct fieldwork on their
537 properties, and D. Josic, J. Berrío-Martínez, V. Flores, M. Le Chevallier, B. Cassens, N.
538 Duda, R. Crisp, M. Nowak, and G. Cohen for their assistance during field work. We are
539 grateful to M. Knörnschild and A. Fernandez for supporting the collection and analysis of
540 acoustic data, I. Waurick for her valuable assistance and expertise during molecular lab
541 work, R. Crisp for observations of co-feeding, and I. Razik and E. Siebert for creating the
542 line drawings in Figure 1 (I.R.: cattle, tree; E.S.: bats). We thank D. Dechmann, J. Kohles, A.
543 Fernandez, and J. Wilkinson for providing valuable feedback on earlier versions of this
544 manuscript.

545 **Literature**

- 546
- 547 Borgeaud C, Bshary R, 2015. Wild vervet monkeys trade tolerance and specific coalitionary support
548 for grooming in experimentally induced conflicts. *Curr Biol* 25:3011-3016.
- 549 Carter GG, Farine DR, Crisp RJ, Vrtillek JK, Ripperger SP, Page RA, 2020. Development of new food-
550 sharing relationships in vampire bats. *Curr Biol* 30:1275-1279. e1273.
- 551 Carter GG, Logsdon R, Arnold BD, Menchaca A, Medellín RA, 2012. Adult vampire bats produce
552 contact calls when isolated: acoustic variation by species, population, colony, and individual.
553 *Plos One* 7:e38791.
- 554 Carter GG, Wilkinson GS, 2013. Food sharing in vampire bats: reciprocal help predicts donations
555 more than relatedness or harassment. *Proc R Soc B* 280:20122573.
- 556 Carter GG, Wilkinson GS, 2015. Social benefits of non-kin food sharing by female vampire bats. *Proc R*
557 *Soc B* 282:20152524.
- 558 Carter GG, Wilkinson GS, 2016. Common vampire bat contact calls attract past food-sharing partners.
559 *Anim Behav* 116:45-51.
- 560 Crespo RF, Fernández SS, Burns RJ, Mitchell GC, 1974. Observaciones sobre el comportamiento del
561 vampiro común (*Desmodus rotundus*) al alimentarse en condiciones naturales. *Revista*
562 *Mexicana de Ciencias Pecuarias* 1:39.
- 563 Cvikel N, Egert Berg K, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y, 2015. Bats
564 aggregate to improve prey search but might be impaired when their density becomes too
565 high. *Curr Biol* 25:206-211. doi: <http://dx.doi.org/10.1016/j.cub.2014.11.010>.
- 566 Dechmann DK, Heucke SL, Giuggioli L, Safi K, Voigt CC, Wikelski M, 2009. Experimental evidence for
567 group hunting via eavesdropping in echolocating bats. *Proceedings of the Royal Society of*
568 *London B: Biological Sciences:rsob*. 2009.0473.
- 569 Dechmann DK, Kranstauber B, Gibbs D, Wikelski M, 2010. Group hunting—a reason for sociality in
570 molossid bats? *Plos One* 5:e9012.
- 571 Delpietro H, Russo R, Carter G, Lord R, Delpietro G, 2017. Reproductive seasonality, sex ratio and
572 philopatry in Argentina's common vampire bats. *Royal Society open science* 4:160959.
- 573 Di Tosto G, Paolucci M, Conte R, 2007. Altruism among simple and smart vampires. *International*
574 *Journal of Cooperative Information Systems* 16:51-66.
- 575 Egert-Berg K, Hurme ER, Greif S, Goldstein A, Harten L, Flores-Martínez JJ, Valdés AT, Johnston DS,
576 Eitan O, Borissov I, 2018. Resource ephemerality drives social foraging in bats. *Curr Biol*
577 28:3667-3673. e3665.
- 578 Emery NJ, Seed AM, Von Bayern AM, Clayton NS, 2007. Cognitive adaptations of social bonding in
579 birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:489-505.
- 580 Farine DR, 2013. Animal social network inference and permutations for ecologists in R using asnipe.
581 *Methods in Ecology and Evolution* 4:1187-1194. doi: 10.1111/2041-210X.12121.
- 582 Farine DR, Carter GG, 2020. Permutation tests for hypothesis testing with animal social data:
583 problems and potential solutions. *BioRxiv*.
- 584 Firth JA, Voelkl B, Farine DR, Sheldon BC, 2015. Experimental evidence that social relationships
585 determine individual foraging behavior. *Curr Biol* 25:3138-3143.
- 586 Foster KR, 2004. Diminishing returns in social evolution: the not-so-tragic commons. *J Evol Biol*
587 17:1058-1072.
- 588 Fruteau C, Voelkl B, Van Damme E, Noë R, 2009. Supply and demand determine the market value of
589 food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences*
590 106:12007-12012.
- 591 Greenhall AM, 1972. The biting and feeding habits of the vampire bat, *Desmodus rotundus*. *J Zool*
592 168:451-461.
- 593 Greenhall AM, Schmidt U, Lopez-Forment W, 1971. Attacking behavior of the vampire bat, *Desmodus*
594 *rotundus*, under field conditions in Mexico. *Biotropica*:136-141.
- 595 King AJ, Clark FE, Cowlshaw G, 2011. The dining etiquette of desert baboons: the roles of social
596 bonds, kinship, and dominance in co-feeding networks. *Am J Primatol* 73:768-774.

- 597 Lang SD, Farine DR, 2017. A multidimensional framework for studying social predation strategies.
598 Nature ecology & evolution 1:1230-1239.
- 599 Leoni J, Tanelli M, Strada SC, Berger-Wolf T, 2020. Ethogram-based automatic wild animal monitoring
600 through inertial sensors and GPS data. Ecological Informatics 59:101112.
- 601 Lewanzik D, Sundaramurthy AK, Goerlitz HR, 2019. Insectivorous bats integrate social information
602 about species identity, conspecific activity and prey abundance to estimate cost–benefit ratio
603 of interactions. J Anim Ecol 88:1462-1473.
- 604 Machado AMdS, Cantor M, Costa AP, Righetti BP, Bezamat C, Valle-Pereira JV, Simões-Lopes PC,
605 Castilho PV, Daura-Jorge FG, 2019. Homophily around specialized foraging underlies dolphin
606 social preferences. Biol Lett 15:20180909.
- 607 Radford AN, Majolo B, Aureli F, 2016. Within-group behavioural consequences of between-group
608 conflict: a prospective review. Proceedings of the Royal Society B: Biological Sciences
609 283:20161567.
- 610 Ripperger S, Duda N, Koelpin A, Carter G, 2020a. Simultaneous Monitoring of the Same Animals with
611 PIT Tags and Sensor Nodes Causes No System Interference. Animal Behavior and Cognition
612 7:531-536. doi: <https://doi.org/10.26451/abc.07.04.05.2020>.
- 613 Ripperger SP, Carter GG, Duda N, Koelpin A, Cassens B, Kapitza R, Josic D, Berrío-Martínez J, Page RA,
614 Mayer F, 2019. Vampire bats that cooperate in the lab maintain their social networks in the
615 wild. Curr Biol 29:4139-4144. e4134.
- 616 Ripperger SP, Carter GG, Page RA, Duda N, Koelpin A, Weigel R, Hartmann M, Nowak T, Thielecke J,
617 Schadhauer M, Robert J, Herbst S, Meyer-Wegener K, Wägemann P, Schröder-Preikschat W,
618 Cassens B, Kapitza R, Dressler F, Mayer F, 2020b. Thinking small: next-generation sensor
619 networks close the size gap in vertebrate biologging. PLoS Biol 18:e3000655.
- 620 Roberts G, 2005. Cooperation through interdependence. Anim Behav 70:901-908.
- 621 Robichaud D, Lefebvre L, Robidoux L, 1996. Dominance affects resource partitioning in pigeons, but
622 pair bonds do not. Canadian journal of zoology 74:833-840.
- 623 Sailer H, Schmidt U, 1978. Die sozialen Laute der Gemeinen Vampirfledermaus *Desmodus rotundus*
624 bei Konfrontation am Futterplatz unter experimentellen Bedingungen. Zeitschrift für
625 Säugetierkunde 43:249-261.
- 626 Samuni L, Preis A, Mielke A, Deschner T, Wittig RM, Crockford C, 2018. Social bonds facilitate
627 cooperative resource sharing in wild chimpanzees. Proceedings of the Royal Society B
628 285:20181643.
- 629 Sazima I, 1978. Aspectos do comportamento alimentar dos morcegos hematófago, *Desmodus*
630 *rotundus*. Boletim de Zoologia 3:97-120.
- 631 Schmidt U, 1978. Vampirfledermäuse. Wittenberg Lutherstadt: A. Ziemsen Verlag.
- 632 Seed AM, Clayton NS, Emery NJ, 2008. Cooperative problem solving in rooks (*Corvus frugilegus*).
633 Proceedings of the Royal Society B: Biological Sciences 275:1421-1429.
- 634 Sierro J, Loretto MC, Szípl G, Massen JJ, Bugnyar T, 2020. Food calling in wild ravens (*Corvus corax*)
635 revisited: Who is addressed? Ethology 126:257-266.
- 636 Szípl G, Boeckle M, Wascher CA, Spreafico M, Bugnyar T, 2015. With whom to dine? Ravens'
637 responses to food-associated calls depend on individual characteristics of the caller. Anim
638 Behav 99:33-42.
- 639 West SA, Gardner A, Shuker DM, Reynolds T, Burton-Chellow M, Sykes EM, Guinnee MA, Griffin AS,
640 2006. Cooperation and the scale of competition in humans. Curr Biol 16:1103-1106.
- 641 Wilkinson GS, 1984. Reciprocal food sharing in the vampire bat. Nature 308:181.
- 642 Wilkinson GS, 1985. The social organization of the common vampire bat - I. Pattern and cause of
643 association. Behav Ecol Sociobiol 17:111-121.
- 644 Wilkinson GS, 1988. Social organization and behavior. Natural history of vampire bats (AM Greenhall
645 and U Schmidt, eds) CRC Press, Boca Raton, Florida:85-98.
- 646 Wilkinson GS, Boughman JW, 1998. Social calls coordinate foraging in greater spear-nosed bats. Anim
647 Behav 55:337-350.
- 648 Witkowski M, 2007. Energy sharing for swarms modeled on the common vampire bat. Adapt Behav
649 15:307-328.

