

# 1 Kinship, association and social complexity in bats

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24 **Abstract**

25 Among mammals, bats exhibit extreme variation in sociality, with some species living  
26 largely solitary lives while others form colonies of more than a million individuals. Some  
27 tropical species form groups during the day that persist throughout the year while many  
28 temperate species only gather into groups during hibernation or parturition. How groups  
29 form and then persist has now been described for a number of species, but the degree to  
30 which kinship explains patterns of association has never been quantified across species.  
31 Here we use social network analysis and genetic data to determine the extent to which  
32 relatedness contributes to associations among individuals estimated from free-ranging  
33 animals across nine species from four families of bats. Network analysis reveals that all  
34 species show evidence of emergent social structure. Variation in the strength of the  
35 relationship between genetic relatedness and social association appears to be related to  
36 the degree of roost switching, i.e. species in which individuals change roosts frequently  
37 tend to exhibit higher levels of association among relatives. Sex-biased dispersal  
38 determines whether associations were between male or female relatives. The strength of  
39 associations among kin does not predict known occurrence of complex behaviors, such as  
40 dominance or various types of cooperation, indicating that kinship is not a prerequisite  
41 for social complexity in bats.

42

43 **Significance statement**

44 The number of differentiated relationships has been proposed as a way to measure social  
45 complexity. Among primates, relationships can be differentiated on the basis of rank, age,  
46 kinship, or association. Application of this approach to other groups of mammals that

47 vary in sociality could help reveal ecological, behavioral or cognitive similarities and  
48 differences between species. As a first step toward this approach, we used social network  
49 analysis on long-term individual records and estimated relatedness using genetic markers  
50 for nine species of bats. We confirmed non-random emergent social structure in all  
51 species. Kinship was predictive of social association among individuals of the same sex  
52 in a few species, but largely independent of the occurrence of complex behaviors, such as  
53 dominance among males or cooperation among females. Complex social behavior in bats  
54 appears to require frequent interactions among a small number of individuals that roost  
55 together for multiple years.

56

## 57 **Keywords**

58 Social networks, kinship, modularity, fission-fusion, cooperation

59

## 60 **Introduction**

61 Social complexity is often associated with cooperative breeding, especially among insects  
62 and birds (Avilés and Harwood 2012; Kappeler 2018). Cooperative breeding also occurs  
63 in a few mammal species, e.g. some mole rats (Jarvis 1981; Bennett et al. 1996),  
64 mongooses (Creel and Creel 1991; Bell et al. 2012; Bell et al. 2014), and canids (Creel et  
65 al. 1997; Moehlman and Hofer 1997). In each of these cases, some individuals forego  
66 reproduction and provide assistance to closely related reproductives in a group (Clutton-  
67 Brock et al. 2001; Clutton-Brock et al. 2010). Multiple close kin are present because they  
68 are born together in a litter from a single-mated female and then remain in an extended  
69 family group (Lukas and Clutton-Brock 2012). Cooperative breeding has not been

70 reported in monotonous species, such as most cetaceans, elephants, and primates, despite  
71 their frequent inclusion in discussions of social complexity (e.g. Connor et al. 1998;  
72 Payne 2003; MacKinnon and Fuentes 2011). In contrast, these species are more likely to  
73 exhibit less costly social behaviors, such as alloparental care (Lee 1987; Packer et al.  
74 1992, Roulin, 2002 #188; MacLeod and Lukas 2014), information exchange (McComb et  
75 al. 2001; Brent et al. 2015), or more complex interactions, such as alliance forming  
76 (Seyfarth and Cheney 1984; Connor et al. 1992; Chapais 1995; Silk et al. 2004;  
77 Wiszniewski et al. 2012). These interactions sometimes, but not always, involve related  
78 individuals (Moller et al. 2001; Parsons et al. 2003; Schino and Aureli 2010) and can  
79 have fitness benefits (Silk 2007). Thus, the extent to which social complexity requires  
80 cooperative breeding depends on how social complexity is defined. When the definition  
81 focuses on the number of differentiated relationships (sensu Freeberg et al. 2012;  
82 Bergman and Beehner 2015), the degree to which interactions involve close relatives is  
83 an open question.

84         A first step in assessing the complexity of a social system (sensu Kappeler 2018)  
85 is to test if patterns of association between individuals occur at random. The extent to  
86 which individuals preferentially associate with others over extended periods of time,  
87 especially when moving between many different sites (see He et al. 2018) provides an  
88 indication of the opportunity for repeated and possibly complex interactions. If  
89 nonrandom associations exist, then a second step is to test for a correlation between  
90 association and relatedness, which could arise simply as a byproduct of sex-biased natal  
91 philopatry or as a result of individuals preferentially associating with kin. Where it is  
92 possible to observe individuals interacting repeatedly in multiple contexts, the number

93 and type of differentiated social relationships can provide information on additional  
94 dimensions of social complexity (Bergman and Beehner 2015; Kappeler 2018).

95 Bats provide an interesting group in which to examine kinship, association and  
96 social complexity because they exhibit diverse social systems, from species that roost  
97 solitarily to those that form small groups or large colonies (Bradbury 1977; McCracken  
98 and Wilkinson 2000; Kerth 2008). Many bats also live a long time, with longevities of  
99 multiple species known to exceed 30 years (Wilkinson and South 2002). Long lifespan  
100 enables individuals to interact repeatedly in ways that facilitate cooperation. Examples of  
101 cooperative behaviors among bats include information exchange in Spix's disc-winged  
102 bats, *Thyroptera tricolor* (Chaverri et al. 2010; Chaverri et al. 2013), Watson's fruit-  
103 eating bat, *Dermanura watsoni* (Gillam et al. 2013), Honduran white bats, *Ectophylla*  
104 *alba* (Gillam et al. 2013), Bechstein's bats, *Myotis bechsteinii* (Kerth and Reckardt 2003),  
105 evening bats, *Nycticeius humeralis* (Wilkinson 1992b) and greater spear-nosed bats,  
106 *Phyllostomus hastatus* (Wilkinson and Boughman 1998); huddling for warmth in pallid  
107 bats, *Antrozous pallidus* (Trune and Slobodchikoff 1976) and *M. bechsteinii* (Pretzlaff et  
108 al. 2010); social grooming in vampire bats, *Desmodus rotundus* (Wilkinson 1986; Carter  
109 and Leffer 2015); communal nursing in *N. humeralis* (Wilkinson 1992a), pup guarding in  
110 *P. hastatus* (Bohn et al. 2009); and food sharing in *D. rotundus* (Wilkinson 1984; Carter  
111 and Wilkinson 2013b). While kinship has been implicated in some of these behaviors, it  
112 appears to be unimportant in others (Wilkinson et al. 2016). This should not be surprising  
113 given that bat social structures and life histories more closely resemble those of primates  
114 and cetaceans than mole rats or mongooses.

115           Opportunities for adults to interact with relatives depend on patterns of  
116 reproduction and dispersal. Female bats typically give birth to one or occasionally two  
117 pups each year (Racey and Entwistle 2000) and survival to age of first reproduction  
118 tends to be low (e.g. Tuttle and Stevenson 1982; Storz 2000), which should serve to  
119 lower the likelihood of interacting with relatives as adults. Offspring of one or both sexes  
120 typically disperse in the first year, presumably to avoid inbreeding (Clutton-Brock and  
121 Lukas 2012). All possible sex-biased patterns of dispersal occur in bats. As in most  
122 mammals (Greenwood 1980; Clutton-Brock and Lukas 2012), female philopatry with  
123 male dispersal away from the birth site is common in bats (Castella et al. 2001; Chen et  
124 al. 2008; Moussy et al. 2013). As a consequence, one or more matriline, each with some  
125 close female relatives, can be present in a mixed-sex colony in some tropical species,  
126 such as *D. rotundus* (Wilkinson 1985b), as well as in female maternity colonies of many  
127 temperate species, e.g. pallid bats, *A. pallidus* (Arnold and Wilkinson 2015), northern  
128 long-eared bats, *M. septentrionalis* (Patriquin et al. 2013), and *N. humeralis* (Wilkinson  
129 1992a). However, average relatedness among females in a colony is often very low, e.g.  
130 big brown bats, *Eptesicus fuscus* (Metheny et al. 2007), greater horseshoe bats,  
131 *Rhinolophus ferrumequinum* (Rossiter et al. 2002), and *M. bechsteinii* (Kerth et al. 2002),  
132 and so interactions among relatives requires kin-biased associations. Male philopatry  
133 with female dispersal also occurs in some species, e.g. greater sac-winged bats,  
134 *Saccopteryx bilineata* (Bradbury and Vehrencamp 1976) and proboscis bats,  
135 *Rhynchonycteris naso* (Nagy et al. 2013), resulting in associations among related adult  
136 males. In at least one species, *T. tricolor*, neither sex disperses from their natal groups,  
137 and mating occurs between groups, resulting in closely related males and females

138 roosting together (Chaverri and Kunz 2011; Buchalski et al. 2014). Finally, dispersal of  
139 both sexes has been reported in several species, e.g. *P. hastatus* (McCracken and  
140 Bradbury 1981), *Lophostoma silvicola* (Dechmann et al. 2007), *Cynopterus sphinx* (Storz  
141 2000; Storz et al. 2001b) and *Molossus molossus* (Gager et al. 2016), where a single male  
142 defends a group of unrelated females for periods that exceed the time to sexual maturity.  
143 In these species, adult relatedness is near zero (McCracken 1987; Storz et al. 2001a).

144         While some bat species form large colonies every year at the same traditional  
145 sites, such as particular caves, buildings or trees, in many cavity or crevice roosting  
146 species individuals gather together during the day in small groups, but frequently change  
147 roosting sites and partners (Lewis 1995). Careful monitoring of marked individuals over  
148 time has, nevertheless, revealed the presence of social units defined by repeated roosting  
149 associations in, for example, *Chalinolobus gouldii* (Godinho et al. 2015), *D. rotundus*  
150 (Wilkinson 1985a), *E. fuscus* (Metheny et al. 2007), *Myotis bechsteinii* (Kerth and König  
151 1999; Kerth et al. 2011), *M. daubentonii* (August et al. 2014), *M. septentrionalis*  
152 (Patriquin et al. 2010), and *Nyctalus lasiopterus* (Fortuna et al. 2009). Interestingly, *M.*  
153 *nattereri* forms social units in England (August et al. 2014) but not in Germany (Zeus et  
154 al. 2018). Thus, the social structure of many cavity roosting bats is complex and  
155 resembles other fission-fusion animal societies (Aureli et al. 2008).

156         As in African elephant, *Loxodonta africana* (Archie et al. 2006), giraffe, *Giraffa*  
157 *camelopardalis* (Carter et al. 2013) and wild boar, *Sus scrofa* (Podgorski et al. 2014),  
158 some, but not all, members of bat social units are related (Wilkinson 1985b; Kerth et al.  
159 2002; Metheny et al. 2007; Kerth et al. 2011; Patriquin et al. 2013; Zeus et al. 2018).  
160 These observations suggest that individuals identify members of their social unit using

161 some type of cue or signal that is not strictly associated with kinship. For example, some  
162 species produce particular social calls with distinctive features that permit discrimination  
163 among individuals, such as *T. tricolor* (Gillam and Chaverri 2012), *D. watsoni*, *E. alba*  
164 (Gillam et al. 2013), *A. pallidus* (Arnold and Wilkinson 2011), and *D. rotundus* (Carter et  
165 al. 2012; Carter and Wilkinson 2016), or among groups in *P. hastatus* (Boughman 1997;  
166 Boughman and Wilkinson 1998) and *S. bilineata* (Knörnschild et al. 2012). In other  
167 species, olfactory cues likely serve similar functions, such as in the common pipistrelle,  
168 *Pipistrellus pipistrellus* (Defanis and Jones 1995), the fishing bat, *Noctilio leporinus*  
169 (Brooke and Decker 1996), *M. bechsteinii* (Safi and Kerth 2003) and several molossid  
170 species including *Mops condylurus*, *Chaerophon pumilus*, and *Tadarida brasiliensis*  
171 (Bouchard 2001; Englert and Greene 2009). Intriguingly, recent evidence suggests that  
172 bats possess place cells in their hippocampus that allow them to track social relationships  
173 and proximity to group members (Omer et al. 2018).

174         Determining if a particular species exhibits non-random or kin-biased associations  
175 requires quantitative analyses of association and relatedness. Social network analysis  
176 (Whitehead 2008; Farine and Whitehead 2015) provides a method for comparing social  
177 systems and has been previously applied to bats (Chaverri 2010; Patriquin et al. 2010;  
178 Kerth et al. 2011), but no prior study has attempted to compare social networks and  
179 relatedness across species. For this reason we decided to analyze observational and  
180 genetic data from long-term studies on nine species from four different families of bats.  
181 All nine species roost during the day in distinct sites, such as on or inside furled leaves,  
182 trees, caves, or man-made structures, where interactions, such as allogrooming,  
183 allofeeding, information transfer and mutual warming, would be restricted to individuals

184 sharing the same roosting site. Consequently, observations of uniquely marked  
185 individuals within a roosting site on a given day provide consistency in how data are  
186 collected, making them ideal for comparative network analysis (Farine & Whitehead  
187 2015). Similarly, standard nondestructive tissue sampling (Worthington-Wilmer and  
188 Barratt 1996) provides comparable genetic data for estimating relatedness across datasets  
189 (Wang 2011; Wang 2017).

190         In this study we used estimates of association and relatedness to answer three  
191 questions. First, do males or females form same-sex associations that are more frequent  
192 than expected by chance? We focus on same-sex associations in part because only  
193 females are present at maternity sites and can therefore be compared across all species.  
194 To answer this question, we used randomization methods to determine if the observed  
195 coefficient of variation for the simple ratio index, i.e. the proportion of observations in  
196 which both individuals were seen roosting together, was greater than would be expected  
197 if associations occurred at random (Whitehead 2008; Farine 2017). Second, do  
198 individuals preferentially associate with same-sex relatives? We addressed this question  
199 both by determining if relatedness predicts association among dyads, and by testing if  
200 relatedness predicts membership in a social unit or community, as defined by maximum  
201 modularity in the social network (Girvan and Newman 2002; Newman 2004; Newman  
202 2006). Finally, given that the species differ in the degree to which individuals use more  
203 than one roosting site, we consider if roost-switching influences the patterns of  
204 relatedness and association among species.

205

206 **Methods**

207 *Species*

208 We used original observation and genotype data for the following nine species of bats,  
209 *Rhynchonycteris naso*, *Saccopteryx bilineata* (family Emballonuridae), *Artibeus*  
210 *jamaicensis*, *Phyllostomus hastatus*, *Desmodus rotundus* (family Phyllostomidae),  
211 *Thyroptera tricolor* (family Thyropteridae), *Nycticeius humeralis*, *Myotis bechsteinii*, and  
212 *M. septentrionalis* (family Vespertilionidae). In Online Resource 1 we provide additional  
213 information on study site number, location, capture, marking, observations, and methods  
214 for obtaining tissue samples for each species, and briefly describe methods for scoring  
215 genotypes at polymorphic loci. A table in Online Resource 1 also summarizes the  
216 amount of observational and genetic data used for each species. In several species, data  
217 were only available for females, either because observations were conducted at summer  
218 maternity sites where adult males rarely occur (*N. humeralis*, *M. bechsteinii*, and *M.*  
219 *septentrionalis*) or because comparable data for adult males were not available (*P.*  
220 *hastatus*). It was also not possible to record data blind because our study involved  
221 censuses of marked animals in the field. Below we summarize how we analyzed these  
222 data.

223

224 *General approach*

225 For each species we used observations of uniquely marked adult individuals in a roosting  
226 site on a day to calculate the simple ratio index (SRI) for each dyad (following Hoppitt  
227 and Farine 2018). If individuals were banded as juveniles, we assumed adult age is not  
228 attained until the individual is at least 9 months old. To improve the accuracy of dyadic

229 association estimates, only individuals observed three or more times as adults were  
230 included. We tested for evidence of nonrandom preferred associations using permutation  
231 tests (Farine 2017) applied to the SRI coefficient of variation for either male-male dyads,  
232 female-female dyads, or all dyads. For species with more than 1,000 observations across  
233 multiple years, we estimated standardized lagged association rates across days to assess  
234 temporal effects on associations of each sex (Whitehead 1995). To reduce confounding  
235 spatial associations with temporal associations, we estimated associations among dyads  
236 over periods of one or more years for species with sufficient data. For those species, we  
237 present average values from nonoverlapping two-year periods for each of the network  
238 metrics described below.

239         We used the SRI to create a weighted nondirectional network for same-sex dyads  
240 for each species and sex within each species using Socprog 2.8 (Whitehead 2009). For  
241 each sex we assigned individuals to communities using the Girvan-Newman maximum  
242 modularity method (Girvan and Newman 2002; Newman 2004; Newman 2006). For each  
243 potential grouping, modularity measures the difference between the ratio of the sum of  
244 SRI within a community over the total SRI to the corresponding ratio when individuals  
245 are assigned to communities at random. Modularity values above 0.3 are often used as  
246 evidence for the presence of communities in the network (Whitehead 2009), but note that  
247 simulations suggest this threshold should be 0.5 (Shizuka and Farine 2016).

248         We next computed several descriptive metrics. First, we calculated the network  
249 density, which is the proportion of possible edges observed given the number of  
250 individuals in the network. Second, we estimated two individual-based statistics –  
251 strength and eigenvector centrality –then computed the average of these statistics for each

252 sex within each species. Strength is the sum of edge weights connected to a node, i.e. the  
253 sum of all SRI involving an individual. If individuals in a group are always observed  
254 together, then strength would equal group size minus one. Consequently, we used  
255 strength/(group size - 1) to estimate group stability. Eigenvector centrality is obtained  
256 from the eigenvector of the association matrix, and is a commonly used metric to capture  
257 the degree to which individuals associate with others who have high versus low  
258 associations (Whitehead 2009).

259         To estimate dyadic relatedness we used five different methods in Coancestry  
260 1.0.1.8 (Wang 2011) to analyze genotypes from multiple polymorphic loci. We report the  
261 Wang (2017) estimator because it is unbiased for small samples, but other estimates gave  
262 similar results. We estimated confidence intervals for these estimates using a bootstrap  
263 resampling method (Wang 2011). As expected, the error associated with each dyadic  
264 estimate of relatedness was inversely related to the amount of genetic information  
265 available, i.e. the number of loci and segregating alleles (see Table in Online Resource 1).  
266 For species with relatively few segregating alleles, the estimate for any given dyad was  
267 poor. However, even for species with fewer than 20 segregating alleles, confidence  
268 intervals around estimates for the average relatedness in a community were sufficiently  
269 small to be informative with regard to predicting community membership.

270         We then determined if relatedness predicts association using two methods: (1) a  
271 linear regression quadratic assignment procedure (QAP) via the *asnipe* R package (Farine  
272 2013) to test whether pairwise relatedness predicts dyadic association, and (2) a logistic  
273 regression QAP using the *netlogit* function via the *sna* R package to test whether pairwise  
274 relatedness predicts the probability that both bats in a given dyad are classified as

275 members of the same versus different communities. To enable comparison across all nine  
276 species and reduce potential differences caused by seasonality or mating systems, we  
277 report results for same-sex dyads. To ensure that relatedness estimates were not strongly  
278 influenced by sampling effort, we first extracted the residuals from regressing the  
279 relatedness-association beta coefficient on the sample size of bats for all datasets, and  
280 then predicted these residuals using number of observations per bat as a proxy for  
281 sampling effort. In both cases, the slope estimate was negative and did not significantly  
282 differ from zero; thus, relatedness effects were not driven by sampling effort.

283         To assess the potential effect of roost switching behavior on kinship structure  
284 across species, we tested if the relatedness effect estimates (i.e. regression coefficients)  
285 were predicted by the relative number of roosting sites used per bat. We calculated the  
286 relative number of roosts used for each sex of each species as the number of roosts visited  
287 by each bat divided by the number of total roost observations.

288

#### 289 *Data availability*

290 R code and data for most of the species analyzed in this paper are included in  
291 supplementary material. Data for *Saccopteryx bilineata*, *Rhynchonycteris naso* and  
292 *Myotis bechsteinii* are available from the corresponding author on reasonable request.  
293 Genetic data for *R. naso* is available at <http://dx.doi.org/10.5061/dryad.df878>.

294

295 **Results**

296 *Nonrandom, modular associations by sex*

297 Analysis of the association patterns reveal strong evidence for nonrandom associations in  
298 most sex-species combinations, i.e. the coefficient of variation (CV) for the simple-ratio  
299 index (SRI) for same-sex pairs is greater than expected from random associations (Table  
300 1). The only exceptions to this pattern are female *N. humeralis*, which were observed at a  
301 single site, and female *A. jamaicensis*, which were observed in 20 sites in two caves. In  
302 addition, modularity was greater than 0.3 for all sex-species categories except for female  
303 *A. jamaicensis*, female *M. septentrionalis* and female *M. bechsteinii*. Network diagrams  
304 for those species (Online Resource 2) provide evidence for some consistent clusters of  
305 individuals, but also considerable associations among females across the broader  
306 population. Together, these data provide strong evidence for nonrandom social structure  
307 created by the presence of detectable communities in most species.

308         Interestingly, even though the number of roosting sites varied from 1 to 184 (see  
309 Online Resource 1), the number of communities ranged only from 2 to 8. Community  
310 size estimates varied from seven male and female *T. tricolor* to over 45 female *N.*  
311 *humeralis* (Table 1). Even though observations of *N. humeralis* were limited to a single  
312 roost, two communities were detected (see Online Resource 2) because sets of  
313 individuals were occasionally absent simultaneously from the primary roost, presumably  
314 because they spent time in one or more secondary roosts. Remarkably, the network for *N.*  
315 *humeralis* most closely resembles the network for *M. bechsteinii* (see Online Resource 2)  
316 even though females in the latter species moved among 78 different roost boxes. In  
317 contrast, the number of communities for males and females of the two emballonurid

318 species, *R. naso* and *S. bilineata*, were the same as the number of roosting sites observed  
319 in a given year, because the bats rarely moved between roosting sites during the study  
320 (Table 1). Examination of the network for *R. naso* clearly shows that the communities are  
321 defined by the roosting sites (Figure 1a).

322 For those species where both males and females were observed, comparison of  
323 network densities showed that female-female associations were more common than male-  
324 male associations in the two phyllostomid bats, *D. rotundus* and *A. jamaicensis*. In  
325 contrast, network densities for males and females of the two emballonurids and *T.*  
326 *tricolor* (Table 1) were nearly identical. Female-female communities were larger than  
327 male-male communities for most species except *T. tricolor*. In this species, communities  
328 typically contained nearly equal numbers of individuals of both sexes (Table 1). *T.*  
329 *tricolor* also had the most unique network structure in that individuals of both sexes  
330 rarely associated with same-sex individuals from other communities (Figure 1b). By  
331 contrast, despite having well-defined communities, female vampire bats frequently  
332 roosted with females from other communities (Figure 1c). Male vampire bats were  
333 observed in a fewer number of roosts, so they had a lower network density and formed a  
334 greater number of communities (Figure 1d).

335 Group stability, as measured by the degree to which average node strength equals  
336 group size minus one, varied from 0.13 in male *D. rotundus* to 0.89 in male *S. bilineata*  
337 (Table 2). Group stability was also typically greater in female-female networks than  
338 male-male networks, except in the two emballonurid species where it was higher in males  
339 and *A. jamaicensis* where it was similar in males and females.

340

341 *Sex differences in temporal associations*

342 In the four species where sufficient data were available, we estimated standardized time-  
343 lagged same-sex associations for each sex. This metric estimates the probability that if  
344 two individuals are associated at any time, then, after the specified lag, the second  
345 individual is a chosen associate of the first. In all cases where data were available for  
346 both sexes, standardized lagged association rates among females remained above null  
347 expectations for longer periods of time than standardized lagged association rates among  
348 males (Figure 2). For *R. naso* males, time-lags greater than three years had standardized  
349 lagged association rates comparable to random expectation, while female standardized  
350 lagged association rates remained above random levels after 1200 days. In *S. bilineata*,  
351 time-lags of 600 days resulted in standardized lagged association rates equal to random  
352 expectation levels for males but not for females. Similarly, in *D. rotundus*, male  
353 standardized lagged association rates reached random expectation by 600 days, at which  
354 point female standardized lagged association rates were still well above null expectations.  
355 For comparison, standardized lagged association rates for female *M. bechsteinii* reached  
356 null expectation after three years. Thus, in all four species, interactions among females  
357 appear to be maintained for much longer periods of time than among males.

358

359 *Relatedness and association*

360 For same-sex dyads, relatedness predicted association in female-female dyads in *D.*  
361 *rotundus* and *M. bechsteinii*, among male-male dyads in *A. jamaicensis*, and both female-  
362 female and male-male dyads in *T. tricolor* (Figure 3). In addition, examination of the *T.*

363 *tricolor* data reveals that some males that exhibit high levels of association were  
364 unrelated while unrelated females rarely exhibited high levels of association (Figure 4).

365         Given that the relationships illustrated in Figure 3 used all possible same-sex  
366 dyads, we wanted to determine if relatedness could be used to assign individuals to the  
367 communities defined by maximizing modularity. This analysis produced results similar to  
368 the matrix regression approach (Figure 5a), except that this method detected an effect of  
369 relatedness on the probability of male-male *R. naso* dyads being in the same community.  
370 In addition, because this analysis provides estimates for both the mean of, and variation  
371 in, within-community relatedness, it is possible to compare average within-community  
372 relatedness across species. Most notably, the within-community relatedness in *T. tricolor*  
373 is more than twice as high as any other species (Figure 5b).

374         To determine if patterns of kin-based association could be influenced by  
375 movement among roosts, we first calculated the relative rate of roost switching as the  
376 number of roosts used by each bat (Table 1) divided by the number of observed roost  
377 sites visited by any bat to control for sampling effort. We then tested if the relative rate of  
378 roost switching predicted the relationship between relatedness and association. We found  
379 that the strength of the relationship between relatedness and association, as measured by  
380 either the QAP regression coefficient ( $t = 8.94$ ,  $P < 0.0001$ ) or the logistic regression  
381 coefficient ( $t = 7.22$ ,  $P < 0.0001$ ), was greater when bats visited more roosts (Figure 6).

382

### 383 **Discussion**

384 Social network analysis has been widely used to quantify relationships among individuals  
385 within a species (Whitehead 2008). Rarely, however, has it been used to compare social

386 relationships among species (but see Kudo and Dunbar 2001; Pasquaretta et al. 2014)  
387 because methods often differ among investigators and by species. Because many  
388 echolocating bats spend the day in roosting sites, observations of bats roosting together  
389 on a day provide a common metric for measuring associations. In this study, we used  
390 such data, in conjunction with genetic data, to determine if relatedness influences patterns  
391 of association in nine species of bats.

392

### 393 *Patterns of association and roosting behavior*

394 Many species of bats change roosts often, sometimes on a daily basis (Lewis 1995). In  
395 other species, individuals consistently return to traditional roosting sites over many days  
396 or even years. In this study, we have examples of both types of movement patterns. In the  
397 two emballonurid species, *R. naso* and *S. bilineata*, the number of communities (Table 2)  
398 is close to the number of roosting sites (Table 1) and individual bats rarely moved  
399 between sites. However, in both species, more communities are predicted for males than  
400 for females. Males of these species also exhibit faster decay in lagged associations than  
401 females (Figure 2). Examination of the composition of the predicted male communities  
402 reveals that the presence of more communities than sites is a consequence of low  
403 associations across years among males at some sites. When data for a single year are  
404 analyzed (data not shown), the number of communities matches the number of sites for  
405 males of both emballonurid bat species. The two emballonurid species can occupy roost  
406 sites for many years. Consequently, it is possible that their social associations could result  
407 from passive attraction to a favorite or familiar roosting site rather than to preferred  
408 individuals. For species that do not switch roosts often, it is difficult to disentangle

409 preferred sites and preferred conspecifics because individuals might prefer roosting sites  
410 because of the particular conspecifics located there.

411 In *N. humeralis*, modularity analysis revealed two communities, but both were  
412 detected in a single common roost site. In this case, some bats used at least one other  
413 unobserved roost during the observation period. Additional observations of radio-tagged  
414 *N. humeralis*, indicate that some individuals do switch roosts together and occupy hollow  
415 trees as well as attics (Wilkinson 1992b), providing additional evidence that associations  
416 in this species are not due solely to occupancy of a single roost site.

417 Even though two of the phyllostomid species are similar in that females form  
418 groups year round in cave ceiling depressions, they differ with respect to group stability.  
419 In *A. jamaicensis* females show little fidelity to a site and frequently switch groups, i.e.  
420 they had low modularity and low stability (Table 1). In contrast, *P. hastatus* females  
421 show much higher modularity and fairly high stability. Previous studies reported that  
422 female *P. hastatus* remain together for multiple years independent of the identity of the  
423 harem male or the group's physical location within the cave (McCracken and Bradbury  
424 1981). Our data are largely consistent with this description with the exception of  
425 occasional movement between groups perhaps as a consequence of the greater number of  
426 groups (20 vs. 3) in the cave than in the earlier study at the same site (McCracken and  
427 Bradbury 1981).

428 In all species that roost in hollow tree cavities, community members use multiple  
429 roosts, so nonrandom associations are evidence of social preferences rather than  
430 attraction to a mutually preferred site. In *D. rotundus*, females formed larger same-sex  
431 communities and moved between more roosting sites than males. In the two tree-roosting

432 *Myotis* species, females always roosted with others, but the composition of the roosting  
433 aggregation often changed. These fission-fusion dynamics, also observed in primates and  
434 other species (Aureli et al. 2008), appear to be common in cavity-dwelling bat species  
435 (Metheny et al. 2007; August et al. 2014; Garg et al. 2018; Zeus et al. 2018).

436 Table 1 shows that nearly every species forms non-random associations in which  
437 communities can be identified even though roost sites could typically accommodate a  
438 larger number of individuals than are found (although it might be difficult for many more  
439 *T. tricolor* individuals to roost in a single rolled leaf). Communities are not fully  
440 segregated. In *D. rotundus*, *M. septentrionalis*, and *M. bechsteinii*, for example, members  
441 of two communities also roosted together. These observations are consistent with a  
442 hierarchical social organization, such as has been described for some primates (e.g.  
443 Dunbar 1983) and African elephants (Wittemyer et al. 2009), that is independent of  
444 spatial drivers (see Farine and Sheldon 2016; He et al. 2018).

445 Larger groups can facilitate exchange of information, such as the location of  
446 difficult-to-discover prey patches (Aplin et al. 2012), but also transmission of pathogens  
447 among more individuals (Craft 2015; Sah et al. 2017). These conflicting pressures might  
448 be acute for vampire bats, which sometimes take turns feeding from the same difficult-to-  
449 locate prey animal (Wilkinson 1985a), but are also at risk of rabies transmission  
450 (Blackwood et al. 2013; Johnson et al. 2014). The potential costs associated with a larger  
451 and more highly connected network could explain why network densities were below  
452 50% for every species except *N. humeralis* and *M. bechsteinii*. As a consequence, the  
453 mean association index was also low due to many dyads rarely being found together.  
454 Whether larger aggregations represent passive occupancy of a convenient roost site or

455 whether they enable social interactions with fitness consequences is worthy of further  
456 study.

457       Formation of a community independent of a roosting site requires that group  
458 members find and recognize each other at night. Playback studies have shown that social  
459 calls emitted by *M. bechsteinii* and *M. nattereri* attract conspecifics to roost sites  
460 (Schöner et al. 2010). Simple attraction to conspecifics could lead to group formation, but  
461 not necessarily stable associations, which require individual or group-level  
462 discrimination. Several species of bats give or exchange vocalizations prior to joining a  
463 roosting group and these vocalizations often are individually distinctive (Arnold and  
464 Wilkinson 2011; Carter et al. 2012; Gillam and Chaverri 2012; Gillam et al. 2013). This  
465 type of recognition system is likely to be a prerequisite for more complex behaviors.

466

#### 467 *Patterns of association and relatedness*

468 We found that relatedness predicts same-sex association largely in accordance with  
469 patterns expected from interspecific variation in dispersal (Table 2). In *R. naso*, *S.*  
470 *bilineata* and *A. jamaicensis*, where females are more likely to disperse (Ortega et al.  
471 2003; Nagy et al. 2012; Nagy et al. 2013), relatedness is more likely to predict group  
472 assignment in males than females. In contrast, in the species where males disperse, which  
473 includes the three temperate vespertilionid species and the vampire bat, *D. rotundus*,  
474 females are more likely to form communities with female relatives. In species where both  
475 sexes disperse, such as *P. hastatus*, relatedness does not influence association. Finally, in  
476 the disk-winged bats, *T. tricolor*, relatedness is a strong predictor of association in both  
477 males and in females. These bats are perhaps most similar to killer whales, *Orcinus orca*

478 (Parsons et al. 2009) in that females and males remain with their mother, but mating  
479 occurs between groups (Chaverri and Kunz 2011). Both sexes also show high levels of  
480 group stability (cf. Table 1) and have higher average levels of relatedness than any other  
481 species (Fig. 5b). Group stability is maintained by individual-specific vocalizations that  
482 are used to reunite individuals in a new roost every day (Chaverri et al. 2010; Gillam and  
483 Chaverri 2012; Chaverri et al. 2013; Chaverri and Gillam 2015).

484         We did not detect any pattern between the strength of the relationship between  
485 association and relatedness and any feature of the social network. Instead, this  
486 relationship appears to be positively related to the degree of roost switching (cf. Fig. 6).  
487 This result suggests that same-sex communities are more likely to contain relatives in  
488 species where individuals frequently switch roosts. This pattern might be due to young of  
489 the year following matrilineal relatives after they become volant, and then females  
490 continuing to move together in subsequent years. We suspect this pattern will hold for  
491 species in which individuals change roost sites frequently and form stable groups. At  
492 least one other species, the pallid bat (*Antrozous pallidus*), is consistent with this  
493 prediction. In many parts of its range, female pallid bats roost in rock crevices during the  
494 day and often switch roosts daily (Lewis 1996). Colonies contain matrilineal relatives as  
495 a consequence of natal philopatry (Arnold and Wilkinson 2015) and estimates of  
496 relatedness among adult females in those groups is significantly higher than expected if  
497 groups formed at random (Arnold 2011). Similar to *T. tricolor*, pallid bats give contact  
498 calls prior to entering a day roost (Arnold and Wilkinson 2011) and acoustic similarity  
499 between calls correlates with relatedness (Arnold 2011), suggesting that relatives may  
500 find each other using vocalizations. In our study, association predicted relatedness most

501 strongly for female *M. bechsteinii*, female *D. rotundus*, and both sexes of *T. tricolor*. In  
502 contrast, *D. rotundus* males use fewer roost sites than females, form smaller groups, and  
503 are not related. Similarly, in *M. bechsteinii*, solitary males move much less among roosts  
504 than colony-living females (Kerth and Morf 2004). Conversely, we anticipate that stable  
505 groups of unrelated individuals, such as occurs in female *P. hastatus* (McCracken and  
506 Bradbury 1981), require a traditional site to form a community. To our knowledge, data  
507 are not available to determine if association predicts relatedness for bat species that roost  
508 together in large groups and often use multiple sites, such as some flying foxes (Parsons  
509 et al. 2011; Roberts et al. 2012). Comparable data for these species would provide a  
510 useful comparison.

511

#### 512 *Social complexity*

513 Many types of behavioral interactions can impact the fitness of group members and  
514 contribute to social complexity (Freeberg et al. 2012; Bergman and Beehner 2015). While  
515 detailed observational studies on individually marked animals in multiple contexts are not  
516 available for all species included in this study, categorical information exists on the  
517 occurrence of behaviors that mediate conflict, i.e. dominance and cooperative behaviors  
518 (Table 2). These behaviors vary in the degree to which social cognition is required. For  
519 example, in the absence of any morphological correlates, a stable linear dominance  
520 hierarchy requires individual recognition and memory of at least recent interactions.  
521 Thus, categorizing species by types of behavioral interactions can provide information on  
522 an additional dimension of social complexity. Whether relatedness helps to explain any  
523 of this variation is an open question.

524           In several species, dominance relationships have been described among males.  
525   For example, in *P. hastatus*, *D. rotundus*, *S. bilineata*, and *A. jamaicensis*, subordinate  
526   males are excluded from roosts with females that are defended by a single dominant male  
527   (Bradbury and Vehrencamp 1976; Morrison 1979; McCracken and Bradbury 1981;  
528   Wilkinson 1985b; Park 1991; Ortega and Arita 2000; Heckel and von Helversen 2002).  
529   Subordinate males in *A. jamaicensis* are sometimes close relatives of the dominant male  
530   (Ortega et al. 2003). Similarly, in *R. naso*, diurnal roosting groups contain multiple males  
531   and females, but one or two males in a group exhibit dominance with regard to their  
532   nocturnal roosting location and mating (Günther et al. 2016). As in *A. jamaicensis*, male  
533   *R. naso* are often related within a community due to natal philopatry (Nagy et al. 2013).  
534   However, the extent to which any of these dominance relationships extend beyond  
535   categorization of one dominant vs. multiple subordinates and instead result in a linear  
536   hierarchy or an even more complex triadic relationship, such as an alliance, is unclear.  
537   Harem males are typically older in *P. hastatus*, *S. bilineata*, and *D. rotundus*, but  
538   otherwise morphologically indistinguishable, which suggests that age may be important  
539   for attaining dominant status (McCracken and Bradbury 1981; Wilkinson 1985b; Heckel  
540   and von Helversen 2002). Subordinate males in these species also often roost in particular  
541   locations, which could provide spatial cues for recognition.

542           In contrast to reported cases of dominance, most of which involve males, several  
543   different types of potential cooperative behaviors have been described for female bats  
544   (Wilkinson 1987; Kerth 2008; Carter and Wilkinson 2013a). Among the species included  
545   in this study, these behaviors occur predominantly among females that are sometimes, but  
546   not always, related (Table 2). Thus, while natal philopatry can result in related

547 individuals developing associations in bat species that switch roosts frequently,  
548 relatedness does not appear to be necessary for cooperation to arise among individuals  
549 within communities.

550 Evidence from at least two species suggests that persistent relationships can be  
551 important in more than one social context. Female greater spear-nosed bats, *P. hastatus*,  
552 do not roost with relatives (McCracken and Bradbury 1981), but they do use group-  
553 specific vocalizations to forage together (Boughman and Wilkinson 1998; Wilkinson and  
554 Boughman 1998). They also protect nonoffspring pups in their group from infanticidal  
555 females from different groups if pups fall to the cave floor and the mother is absent  
556 (Bohn et al. 2009). Thus, females exhibit group-specific interactions in multiple contexts,  
557 but it is unclear if their responses depend directly on prior interactions. In common  
558 vampire bats, *D. rotundus*, females preferentially regurgitate blood to past roostmates that  
559 fail to obtain a blood meal (Wilkinson 1984). When housed together, food sharing is  
560 predicted by social grooming and reciprocal food sharing more than by relatedness  
561 (Carter and Wilkinson 2013b). Vampire bats also approach playbacks of vocalizations  
562 from unrelated food-sharing partners but not non-sharing relatives (Carter and Wilkinson  
563 2016). Such a response minimally requires individual recognition and memory of the  
564 prior behavior of others. We suspect that more examples of complex social interactions in  
565 bats will be discovered as more detailed social information is collected across multiple  
566 contexts. The degree to which these interactions involve related versus unrelated  
567 individuals will be interesting to discover.

568

569 **Acknowledgements**

570 We thank B. Negash for assistance in preparing data and H. Whitehead, D. Lukas, and P.  
571 Kappeler, as well as several other participants of the Göttinger Freilandtage for useful  
572 suggestions.

573

574 **Compliance with ethical standards**

575 **Conflict of Interest:** The authors declare that they have no conflict of interest.

576 **Ethical approval:** All applicable international, national, and/or institutional guidelines  
577 for the care and use of animals were followed.

578

579 **References**

- 580 Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC (2012) Social networks predict  
581 patch discovery in a wild population of songbirds. *Proc Biol Sci B* 279:4199-4205
- 582 Archie EA, Moss CJ, Alberts SC (2006) The ties that bind: genetic relatedness predicts  
583 the fission and fusion of social groups in wild African elephants. *Proc R Soc Lond*  
584 *B* 273:513-522
- 585 Arnold BD (2011) Social vocalizations and their implications for group dynamics of  
586 pallid bats (*Antrozous pallidus*). Doctoral dissertation, University of Maryland, pp  
587 123
- 588 Arnold BD, Wilkinson GS (2011) Individual specific contact calls of pallid bats  
589 (*Antrozous pallidus*) attract conspecifics at roosting sites. *Beh Ecol Sociobiol*  
590 65:1581-1593

591 Arnold BD, Wilkinson GS (2015) Female natal philopatry and gene flow between  
592 divergent clades of pallid bats (*Antrozous pallidus*). J Mamm 96:531-540

593 August TA, Nunn MA, Fensome AG, Linton DM, Mathews F (2014) Sympatric  
594 woodland *Myotis* bats form tight-knit social groups with exclusive roost home  
595 ranges. PLoS One 9:e112225

596 Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Fiore  
597 AD, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P,  
598 Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, Schaik CPv (2008)  
599 Fission-fusion dynamics: New research frameworks. Curr Anthro 49:627-654

600 Avilés L, Harwood G (2012) A quantitative index of sociality and its application to group  
601 living spiders and other social organisms. Ethology 118:1219-1229

602 Bell MBV, Cant MA, Borgeaud C, Thavarajah N, Samson J, Clutton-Brock TH (2014)  
603 Suppressing subordinate reproduction provides benefits to dominants in  
604 cooperative societies of meerkats. Nat Commun 5

605 Bell MBV, Nichols HJ, Gilchrist JS, Cant MA, Hodge SJ (2012) The cost of dominance:  
606 suppressing subordinate reproduction affects the reproductive success of  
607 dominant female banded mongooses. Proc R Soc Lond B 279:619-624

608 Bennett NC, Faulkes CG, Molteno AJ (1996) Reproductive suppression in subordinate,  
609 non-breeding female Damaraland mole-rats: Two components to a lifetime of  
610 socially induced infertility. Proc R Soc Lond B 263:1599-1603

611 Bergman TJ, Beehner JC (2015) Measuring social complexity. Anim Behav 103:203-209

612 Blackwood JC, Streicker DG, Altizer S, Rohani P (2013) Resolving the roles of  
613 immunity, pathogenesis, and immigration for rabies persistence in vampire bats.  
614 Proc Natl Acad Sci USA 110:20837-42

615 Bohn KM, Moss CF, Wilkinson GS (2009) Pup guarding by greater spear-nosed bats.  
616 Beh Ecol Sociobiol 63:1693-1703

617 Bouchard S (2001) Sex discrimination and roostmate recognition by olfactory cues in the  
618 African bats, *Mops condylurus* and *Chaerephon pumilus* (Chiroptera :  
619 Molossidae). J Zool 254:109-117

620 Boughman JW (1997) Greater spear-nosed bats give group-distinctive calls. Beh Ecol  
621 Sociobiol 40:61-70

622 Boughman JW, Wilkinson GS (1998) Greater spear-nosed bats discriminate group mates  
623 by vocalizations. Anim Behav 55:1717-1732

624 Bradbury JW (1977) Social organization and communication. In: Wimsatt WA (ed) The  
625 Biology of Bats. Academic Press, New York, pp 1-72

626 Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in Emballonurid  
627 bats. I. Field studies. Behav Ecol Sociobiol 1:337-381

628 Brent LJ, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP (2015) Ecological  
629 knowledge, leadership, and the evolution of menopause in killer whales. Curr Biol  
630 25:746-50

631 Brooke AP, Decker DM (1996) Lipid compounds in secretions of fishing bat, *Noctilio*  
632 *leporinus* (Chiroptera: Noctilionidae). J Chem Ecol 22:1411-28

633 Buchalski MR, Chaverri G, Vonhof MJ (2014) When genes move farther than offspring:  
634 gene flow by male gamete dispersal in the highly philopatric bat species  
635 *Thyroptera tricolor*. *Mol Ecol* 23:464-80

636 Carter G, Leffer L (2015) Social grooming in bats: are vampire bats exceptional? . *PLoS*  
637 *ONE* 10:e0138430

638 Carter GG, Logsdon R, Arnold BD, Menchaca A, Medellin RA (2012) Adult vampire  
639 bats produce contact calls when isolated: acoustic variation by species,  
640 population, colony, and individual. *Plos One* 7

641 Carter GG, Wilkinson GS (2013a) Cooperation and conflict in the social lives of bats. In:  
642 Adams RA, Pedersen SC (eds) *Bat Evolution, Ecology, and Conservation*.  
643 Springer Science Press, New York, pp 225-242

644 Carter GG, Wilkinson GS (2013b) Food sharing in vampire bats: reciprocal help predicts  
645 donations more than relatedness or harassment. *Proc R Soc Lond B* 280

646 Carter GG, Wilkinson GS (2016) Common vampire bat contact calls attract past food-  
647 sharing partners. *Anim Behav* 116:45-51

648 Carter KD, Brand R, Carter JK, Shorrocks B, Goldizen AW (2013) Social networks,  
649 long-term associations and age-related sociability of wild giraffes. *Anim Behav*  
650 86:901-910

651 Castella V, Ruedi M, Excoffier L (2001) Contrasted patterns of mitochondrial and  
652 nuclear structure among nursery colonies of the bat *Myotis myotis*. *J Evol Biol*  
653 14:708-720

654 Chapais B (1995) Alliances as a means of competition in primates: Evolutionary,  
655 developmental, and cognitive aspects. *Yearb Phys Anthropol* 38:115-136

656 Chaverri G (2010) Comparative social network analysis in a leaf-roosting bat. *Beh Ecol*  
657 *Sociobiol* 64:1619-1630

658 Chaverri G, Gillam EH (2015) Repeatability in the contact calling system of Spix's disc-  
659 winged bat (*Thyroptera tricolor*). *R Soc open science* 2

660 Chaverri G, Gillam EH, Kunz TH (2013) A call-and-response system facilitates group  
661 cohesion among disc-winged bats. *Beh Ecol* 24:481-487

662 Chaverri G, Gillam EH, Vonhof MJ (2010) Social calls used by a leaf-roosting bat to  
663 signal location. *Biol lett* 6:441-4

664 Chaverri G, Kunz TH (2011) All-offspring natal philopatry in a Neotropical bat. *Anim*  
665 *Behav* 82:1127-1133

666 Chen S-F, Jones G, Rossiter SJ (2008) Sex-biased gene flow and colonization in the  
667 Formosan lesser horseshoe bat: inference from nuclear and mitochondrial  
668 markers. *J Zool* 274:207-215

669 Clutton-Brock TH, Hodge SJ, Flower TP, Spong GF, Young AJ (2010) Adaptive  
670 suppression of subordinate reproduction in cooperative mammals. *Am Nat*  
671 176:664-673

672 Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in  
673 female mammals. *Mol Ecol* 21:472-492

674 Clutton-Brock TH, Russell AF, Sharpe LL, Brotherton PNM, McIlrath GM, White S,  
675 Cameron EZ (2001) Effects of helpers on juvenile development and survival in  
676 meerkats. *Science* 293:2446-2449

677 Connor RC, Mann J, Tyack PL, Whitehead H (1998) Social evolution in toothed whales.  
678 *Trends Ecol Evol* 13:228-232

679 Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among  
680 male bottle-nosed dolphins (*Tursiops* Sp). *P Natl Acad Sci USA* 89:987-990

681 Craft ME (2015) Infectious disease transmission and contact networks in wildlife and  
682 livestock. *Philos T R Soc B* 370

683 Creel S, Creel NM, Mills MGL, Monfort SL (1997) Rank and reproduction in  
684 cooperatively breeding African wild dogs: Behavioral and endocrine correlates.  
685 *Beh Ecol* 8:298-306

686 Creel SR, Creel NM (1991) Energetics, reproductive suppression and obligate communal  
687 breeding in carnivores. *Beh Ecol Sociobiol* 28:263-270

688 Dechmann DKN, Kalko EKV, Kerth G (2007) All-offspring dispersal in a tropical  
689 mammal with resource defense polygyny. *Beh Ecol Sociobiol* 61:1219-1228

690 Defanis E, Jones G (1995) The role of odor in the discrimination of conspecifics by  
691 pipistrelle bats. *Anim Behav* 49:835-839

692 Dunbar RIM (1983) Structure of gelada baboon reproductive units. 2. Social relationships  
693 between reproductive females. *Anim Behav* 31:556-564

694 Englert AC, Greene MJ (2009) Chemically-mediated roostmate recognition and roost  
695 selection by Brazilian free-tailed bats (*Tadarida brasiliensis*). *PLoS One* 4:e7781

696 Farine DR (2013) Animal social network inference and permutations for ecologists in R  
697 using asnipe. *Methods Ecol Evol* 4

698 Farine DR (2017) A guide to null models for animal social network analysis. *Methods*  
699 *Ecol Evol* 8:1309-1320

700 Farine DR, Sheldon BC (2016) Social ecology of a woodland songbird community: from  
701 individual movements to the emergence of population social structure. *bioRxiv*

702 Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social  
703 network analysis. *J Anim Ecol* 84:1144-1163

704 Fortuna MA, Popa-Lisseanu AG, Ibáñez C, Bascompte J (2009) The roosting spatial  
705 network of a bird-predator bat. *Ecology* 90:934-944

706 Freeberg TM, Dunbar RI, Ord TJ (2012) Social complexity as a proximate and ultimate  
707 factor in communicative complexity. *Philos T R Soc B* 367:1785-801

708 Gager Y, Gimenez O, O'Mara MT, Dechmann DKN (2016) Group size, survival and  
709 surprisingly short lifespan in socially foraging bats. *Bmc Ecol* 16

710 Garg KM, Chattopadhyay B, Ramakrishnan U (2018) Social structure in the harem-  
711 forming promiscuous fruit bat, *Cynopterus sphinx*, is the harem truly important?  
712 *R Soc open science*:172024

713 Gillam EH, Chaverri G (2012) Strong individual signatures and weaker group signatures  
714 in contact calls of Spix's disc-winged bat, *Thyroptera tricolor*. *Anim Behav*  
715 83:269-276

716 Gillam EH, Chaverri G, Montero K, Sagot M (2013) Social calls produced within and  
717 near the roost in two species of tent-making bats, *Dermanura watsoni* and  
718 *Ectophylla alba*. *Plos One* 8

719 Girvan M, Newman MEJ (2002) Community structure in social and biological networks.  
720 *P Natl Acad Sci USA* 99:7821-7826

721 Godinho LN, Lumsden LF, Coulson G, Griffiths SR (2015) Network analysis reveals  
722 cryptic seasonal patterns of association in Gould's wattled bats (*Chalinolobus*  
723 *gouldii*) roosting in bat-boxes. *Behav* 152:1079-2105

724 Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals.  
725 Anim Behav 28:1140-1162

726 Günther L, Lopez MD, Knörnschild M, Reid K, Nagy M, Mayer F (2016) From resource  
727 to female defence: the impact of roosting ecology on a bat's mating strategy. R  
728 Soc Open Sci 3:160503

729 He P, Maldonado-Chaparro A, Farine DR (2018) The role of habitat configuration in  
730 shaping social structure: a gap in studies of animal social complexity. Behavioural  
731 Ecology and Sociobiology in press

732 Heckel G, von Helversen O (2002) Male tactics and reproductive success in the harem  
733 polygynous bat *Saccopteryx bilineata*. Beh Ecol 13:750-756

734 Hoppitt W, Farine DR (2018) Association indices for quantifying social relationships:  
735 how to deal with missing observations of individuals or groups. Anim Behav  
736 136:227-238

737 Jarvis JUM (1981) Eusociality in a mammal - cooperative breeding in naked mole-rat  
738 colonies. Science 212:571-573

739 Johnson N, Arechiga-Ceballos N, Aguilar-Setien A (2014) Vampire bat rabies: ecology,  
740 epidemiology and control. Viruses 6:1911-28

741 Kappeler PM (2018) A framework for studying social complexity. Beh Ecol Sociobiol

742 Kerth G (2008) Causes and consequences of sociality in bats. Bioscience 58:737-746

743 Kerth G, König B (1999) Fission, fusion and nonrandom associations in female  
744 Bechstein's bats (*Myotis bechsteinii*). Behav 136:1187-1202

745 Kerth G, Morf L (2004) Behavioural and genetic data suggest that Bechstein's bats  
746 predominantly mate outside the breeding habitat. Ethology 110:987-999

747 Kerth G, Perony N, Schweitzer F (2011) Bats are able to maintain long-term social  
748 relationships despite the high fission-fusion dynamics of their groups. Proc R Soc  
749 Lond B 278:2761-7

750 Kerth G, Reckardt K (2003) Information transfer about roosts in female Bechstein's bats:  
751 an experimental field study. Proc R Soc Lond B 270:511-5

752 Kerth G, Safi K, König B (2002) Mean colony relatedness is a poor predictor of colony  
753 structure and female philopatry in the communally breeding Bechstein's bat  
754 (*Myotis bechsteinii*). Beh Ecol Sociobiol 52:203-210

755 Knörnschild M, Nagy M, Metz M, Mayer F, von Helversen O (2012) Learned vocal  
756 group signatures in the polygynous bat *Saccopteryx bilineata*. Anim Behav  
757 84:761–769

758 Kudo H, Dunbar RIM (2001) Neocortex size and social network size in primates. Anim  
759 Behav 62:711-722

760 Lee PC (1987) Allomothering among African Elephants. Anim Behav 35:278-291

761 Lewis SE (1995) Roost fidelity of bats: a review. J Mamm 76:481-496

762 Lewis SE (1996) Low roost-site fidelity in pallid bats: Associated factors and effect on  
763 group stability. Beh Ecol Sociobiol 39:335-344

764 Lukas D, Clutton-Brock T (2012) Life histories and the evolution of cooperative breeding  
765 in mammals. Proc R Soc Lond B 279:4065-4070

766 MacKinnon KC, Fuentes A (2011) Primates, niche construction, and social complexity:  
767 the roles of social cooperation and altruism. In: Sussman RW, Cloninger CR (eds)  
768 Origins of Altruism and Cooperation. Springer New York, New York, NY, pp  
769 121-143

770 MacLeod KJ, Lukas D (2014) Revisiting non-offspring nursing: allonursing evolves  
771 when the costs are low. *Biol Lett* 10

772 McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories  
773 of social knowledge in African elephants. *Science* 292:491-494

774 McCracken GF (1987) Genetic structure of bat social groups. In: Racey PA, Fenton MB,  
775 Rayner JMV (eds) *Recent advances in the study of bats*. Cambridge University  
776 Press, Cambridge, pp 281-298

777 McCracken GF, Bradbury JW (1981) Social organization and kinship in the polygynous  
778 bat Phyllostomus hastatus. *Behav Ecol Sociobiol* 8:11-34

779 McCracken GF, Wilkinson GS (2000) Bat mating systems. In: Krutzsch PH, Crichton EG  
780 (eds) *Reproductive Biology of Bats*. Academic Press, New York

781 Metheny JD, Kalcounis-Rueppell MC, Willis CKR, Kolar KA, Brigham RM (2007)  
782 Genetic relationships between roost-mates in a fission–fusion society of tree-  
783 roosting big brown bats (*Eptesicus fuscus*). *Behav Ecol Sociobiol* 62:1043-1051

784 Moehlman PD, Hofer H (1997) Cooperative breeding, reproductive suppression, and  
785 body mass in canids. In: Solomon NG, J.A. F (eds) *Cooperative breeding in*  
786 *mammals*. Cambridge University Press, New York, pp 76-128

787 Moller LM, Beheregaray LB, Harcourt RG, Krutzen M (2001) Alliance membership and  
788 kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern  
789 Australia. *Proc R Soc Lond B* 268:1941-1947

790 Morrison DW (1979) Apparent male defense of tree hollows in the bat, Artibeus  
791 jamaicensis. *J Mamm* 60:11-15

792 Moussy C, Hosken DJ, Mathews F, Smith GC, Aegerter JN, Bearhop S (2013) Migration  
793 and dispersal patterns of bats and their influence on genetic structure. *Mamm Rev*  
794 43:183-195

795 Nagy M, Günther L, Knörnschild M, Mayer F (2013) Female-biased dispersal in a bat  
796 with a female-defence mating strategy. *Mol Ecol* 22:1733-45

797 Nagy M, Knörnschild M, Voigt CC, Mayer F (2012) Male greater sac-winged bats gain  
798 direct fitness benefits when roosting in multimale colonies. *Beh Ecol* 23:597-606

799 Newman MEJ (2004) Analysis of weighted networks. *Phys Rev E* 70

800 Newman MEJ (2006) Modularity and community structure in networks. *P Natl Acad Sci*  
801 USA 103:8577-8582

802 Omer DB, Maimon SR, Las L, Ulanovsky N (2018) Social place-cells in the bat  
803 hippocampus. *Science* 359:218-224

804 Ortega J, Arita HT (2000) Defence of females by dominant males of *Artibeus jamaicensis*  
805 (Chiroptera: Phyllostomidae). *Ethology* 106:395-407

806 Ortega J, Maldonado JE, Wilkinson GS, Arita HT, Fleischer RC (2003) Male dominance,  
807 paternity, and relatedness in the Jamaican fruit-eating bat (*Artibeus jamaicensis*).  
808 *Mol Ecol* 12:2409-2415

809 Packer C, Lewis S, Pusey A (1992) A Comparative-Analysis of Nonoffspring Nursing.  
810 *Anim Behav* 43:265-281

811 Park SR (1991) Development of social structure in a captive colony of the common  
812 vampire bat, *Desmodus rotundus*. *Ethology* 89:335-341

813 Parsons JG, Robson SKA, Shilton LA (2011) Roost fidelity in spectacled flying-foxes  
814 *Pteropus conspicillatus*: implications for conservation and management. In: Law

815 B, Eby P, Lunney D, Lumsden L (eds) *The Biology and Conservation of*  
816 *Australasian Bats*. Royal Zoological Society of NSW, Mosman, NSW, pp 66-71

817 Parsons KM, Balcomb KC, Ford JKB, Durban JW (2009) The social dynamics of  
818 southern resident killer whales and conservation implications for this endangered  
819 population. *Anim Behav* 77:963-971

820 Parsons KM, Durban JW, Claridge DE, Balcomb KC, Noble LR, Thompson PM (2003)  
821 Kinship as a basis for alliance formation between male bottlenose dolphins,  
822 *Tursiops truncatus*, in the Bahamas. *Anim Behav* 66:185-194

823 Pasquaretta C, Leve M, Claidiere N, van de Waal E, Whiten A, MacIntosh AJ, Pele M,  
824 Bergstrom ML, Borgeaud C, Brosnan SF, Crofoot MC, Fedigan LM, Fichtel C,  
825 Hopper LM, Mareno MC, Petit O, Schnoell AV, di Sorrentino EP, Thierry B,  
826 Tiddi B, Sueur C (2014) Social networks in primates: smart and tolerant species  
827 have more efficient networks. *Sci Rep* 4:7600

828 Patriquin KJ, Leonard ML, Broders HG, Garroway CJ (2010) Do social networks of  
829 female northern long-eared bats vary with reproductive period and age? *Beh Ecol*  
830 *Sociobiol* 64:899-913

831 Patriquin KJ, Palstra F, Leonard ML, Broders HG (2013) Female northern myotis  
832 (*Myotis septentrionalis*) that roost together are related. *Beh Ecol* 24:949-954

833 Payne K (2003) Sources of social complexity in the three elephant species. In: deWaal  
834 FBM, Tyack PL (eds) *Animal Social Complexity*. Harvard University Press,  
835 Cambridge, MA, pp 57-85

836 Podgorski T, Lusseau D, Scandura M, Sonnichsen L, Jedrzejewska B (2014) Long-  
837 lasting, kin-directed female interactions in a spatially structured wild boar social  
838 network. PLoS One 9:e99875

839 Pretzlaff I, Kerth G, Dausmann KH (2010) Communally breeding bats use physiological  
840 and behavioural adjustments to optimise daily energy expenditure. Naturwiss  
841 97:353-363

842 Racey PA, Entwistle AC (2000) Life history and reproductive strategies of bats. In:  
843 Krutzsch PH, Crichton EG (eds) Reproductive Biology of Bats. Academic Press,  
844 New York

845 Roberts BJ, Catterall CP, Eby P, Kanowski J (2012) Long-distance and frequent  
846 movements of the flying-fox *Pteropus poliocephalus*: implications for  
847 management. PLoS One 7:e42532

848 Rossiter SJ, Jones G, Ransome RD, Barratt EM (2002) Relatedness structure and kin-  
849 biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). Beh  
850 Ecol Sociobiol 51:510-518

851 Safi K, Kerth G (2003) Secretions of the interaural gland contain information about  
852 individuality and colony membership in the Bechstein's bat. Anim Behav 65:363-  
853 369

854 Sah P, Leu ST, Cross PC, Hudson PJ, Bansal S (2017) Unraveling the disease  
855 consequences and mechanisms of modular structure in animal social networks.  
856 Proc Natl Acad Sci USA 114:4165-4170

857 Schino G, Aureli F (2010) The relative roles of kinship and reciprocity in explaining  
858 primate altruism. Ecol Lett 13:45-50

859 Schöner CR, Schöner MG, Kerth G (2010) Similar is not the same: Social calls of  
860 conspecifics are more effective in attracting wild bats to day roosts than those of  
861 other bat species. Beh Ecol Sociobiol 64:2053-2063

862 Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet  
863 monkeys. Nature 308:541-543

864 Shizuka D, Farine DR (2016) Measuring the robustness of network community structure  
865 using assortativity. Anim Behav 112:237-246

866 Silk JB (2007) Social components of fitness in primate groups. Science 317:1347-51

867 Silk JB, Alberts SC, Altmann J (2004) Patterns of coalition formation by adult female  
868 baboons in Amboseli, Kenya. Anim Behav 67:573-582

869 Storz JF (2000) Social structure of a polygynous tent-making bat, *Cynopterus sphinx*  
870 (Megachiroptera). J Zool 251:151-165

871 Storz JF, Bhat HR, Kunz TH (2001a) Genetic consequences of polygyny and social  
872 structure in an Indian fruit bat, *Cynopterus sphinx*. I. Inbreeding, outbreeding,  
873 and population subdivision. Evol 55:1215-1223

874 Storz JF, Bhat HR, Kunz TH (2001b) Genetic consequences of polygyny and social  
875 structure in an Indian fruit bat, *Cynopterus sphinx*. II. Variance in male mating  
876 success and effective population size. Evol 55:1224-1232

877 Trune DR, Slobodchikoff CN (1976) Social effects of roosting on the metabolism of the  
878 pallid bat (*Antrozous pallidus*). J Mamm 57:656-663

879 Tuttle MD, Stevenson D (1982) Growth and survival of bats. In: Kunz TH (ed) Ecology  
880 of Bats. Plenum Press, New York, pp 105-150

881 Wang J (2011) COANCESTRY: a program for simulating, estimating and analysing  
882 relatedness and inbreeding coefficients. *Mol Ecol Resour* 11:141-5

883 Wang J (2017) Estimating pairwise relatedness in a small sample of individuals. *Heredity*  
884 119:302-313

885 Whitehead H (1995) Investigating structure and temporal scale in social organizations  
886 using identified individuals. *Beh Ecol* 6:199-208

887 Whitehead H (2008) Analyzing animal societies: quantitative methods for vertebrate  
888 social analysis. Chicago University Press, Chicago, IL

889 Whitehead H (2009) SOCPROG programs: analysing animal social structures. *Beh Ecol*  
890 *Sociobiol* 63:765-778

891 Wilkinson GS (1984) Reciprocal food sharing in vampire bats. *Nature* 309:181-184

892 Wilkinson GS (1985a) The social organization of the common vampire bat. I. Pattern  
893 and cause of association. *Beh Ecol Sociobiol* 17:111-121

894 Wilkinson GS (1985b) The social organization of the common vampire bat. II. Mating  
895 system, genetic structure, and relatedness. *Beh Ecol Sociobiol* 17:123-134

896 Wilkinson GS (1986) Social grooming in the common vampire bat, Desmodus rotundus.  
897 *Anim Behav* 34:1880-1889

898 Wilkinson GS (1987) Altruism and cooperation in bats. In: Racey PA, Fenton MB,  
899 Rayner JMV (eds) Recent advances in the study of bats. Cambridge University  
900 Press, Cambridge, pp 299-323

901 Wilkinson GS (1992a) Communal nursing in evening bats. *Beh Ecol Sociobiol* 31:225-  
902 235

903 Wilkinson GS (1992b) Information transfer at evening bat colonies. *Anim Behav* 44:501-  
904 518

905 Wilkinson GS, Boughman JW (1998) Social calls coordinate foraging in greater spear-  
906 nosed bats. *Anim Behav* 55:337-350

907 Wilkinson GS, Carter GG, Bohn KM, Adams DM (2016) Non-kin cooperation in bats.  
908 *Philos T R Soc B* 371:20150095

909 Wilkinson GS, South JM (2002) Life history, ecology and longevity in bats. *Aging Cell*  
910 1:124-131

911 Wiszniewski J, Brown C, Moller LM (2012) Complex patterns of male alliance formation  
912 in a dolphin social network. *J Mamm* 93:239-250

913 Wittemyer G, Okello JB, Rasmussen HB, Arctander P, Nyakaana S, Douglas-Hamilton I,  
914 Siegismund HR (2009) Where sociality and relatedness diverge: the genetic basis  
915 for hierarchical social organization in African elephants. *Proc R Soc Lond B*  
916 276:3513-21

917 Worthington-Wilmer J, Barratt EM (1996) A non-lethal method of tissue sampling for  
918 genetic studies of chiropterans. *Bat Res News* 37:1-3

919 Zeus VM, Reusch C, Kerth G (2018) Long-term roosting data reveal a unimodular social  
920 network in large fission-fusion society of the colony-living Natterer's bat (*Myotis*  
921 *nattereri*). *Beh Ecol Sociobiol* 72:99-112

922

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Table 1. Sex-specific association and network metrics by species

Species	Sex	Adults	SRI	CV(SRI)	Density	Strength	Modularity	Communities	Cm size	Stability	Roosts/bat
<i>R. naso</i>	F	45	0.167	1.85***	30.7%	4.92	0.49	3.0	10.2	0.54	1.0
	M	45	0.126	2.03***	29.0%	3.34	0.57	4.0	6.9	0.57	1.1
<i>S. bilineata</i>	F	65	0.112	2.31***	24.2%	2.89	0.67	4.0	7.3	0.46	1.1
	M	41	0.107	2.39***	20.4%	1.55	0.43	6.0	2.8	0.89	1.0
<i>T. tricolor</i>	F	18	0.099	2.33***	23.5%	1.68	0.52	6.0	3.0	0.84	11.6
	M	15	0.136	2.23***	24.8%	1.90	0.66	4.0	3.8	0.69	13.0
<i>A. jamaicensis</i>	F	63	0.028	1.69	31.8%	1.39	0.25	5.0	10.1	0.15	4.9
	M	16	0.023	2.78*	21.0%	0.30	0.45	5.0	3.0	0.15	2.0
<i>P. hastatus</i>	F	97	0.059	2.69*	21.1%	5.64	0.67	7.0	13.9	0.44	1.8
<i>D. rotundus</i>	F	64	0.061	1.87***	45.0%	3.82	0.43	3.0	21.3	0.19	3.1
	M	62	0.021	3.50**	22.7%	1.25	0.55	6.0	10.3	0.13	2.8
<i>N. humeralis</i>	F	97	0.145	1.07	73.0%	13.94	0.32	2.0	48.5	0.29	1.0
<i>M. septentrionalis</i>	F	63	0.057	1.86***	38.7%	3.54	0.20	8.0	7.9	0.52	6.7
<i>M. bechsteini</i>	F	61	0.262	0.77*	90.9%	11.59	0.23	2.5	19.2	0.64	31.6

\*P<0.05, \*\*P<0.01, \*\*\*P < 0.001, randomization

Table 2. Sex-bias in dispersal pattern, relatedness vs. association relationship, and types of behavioral interactions for each species

Species	Dispersing		Dominance	Information	Alloparental	Social	Food
	sex	r vs SRI	hierarchy	exchange	care	grooming	sharing
<i>R. naso</i>	F	M	M				
<i>S. bilineata</i>	F	ns	M				
<i>T. tricolor</i>	Neither*	M, F	?	M, F			
<i>A. jamaicensis</i>	?	M	M			F > M	
<i>P. hastatus</i>	M, F	ns	M	F	F		
<i>D. rotundus</i>	M	F	M	F	F	F > M	F
<i>N. humeralis</i>	M	ns		F	F		
<i>M. septentrionalis</i>	M	ns		F			
<i>M. bechsteinii</i>	M	F		F		F	

\*dispersal of either sex occurs infrequently

## Figure Legends

Figure 1. Network diagrams displaying community identity for A) *Rhynchoycteris naso* from 2013-2014 at three sites, B) *Thyroptera tricolor* from 78 sites, C) *Desmodus rotundus* females and D) males from 15 hollow trees. Line width indicates strength of association. In A and B node color denotes sex (pink = female, blue = male) while in C and D node color denotes community identity. See Online Resource 2 for network diagrams of the other species.

Figure 2. Standardized lagged association rates plotted against time in days for female and male *R. naso*, *S. bilineata*, and *D. rotundus*. Standard errors are estimated by jackknifing. Red lines in each plot indicate standardized null association rates.

Figure 3. Regression slopes obtained from a quadratic assignment procedure for the relationship between association, as measured by the simple-ratio index, plotted against relatedness, using the Wang (2017) estimator, for males and females of each species. Significance is indicated as \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

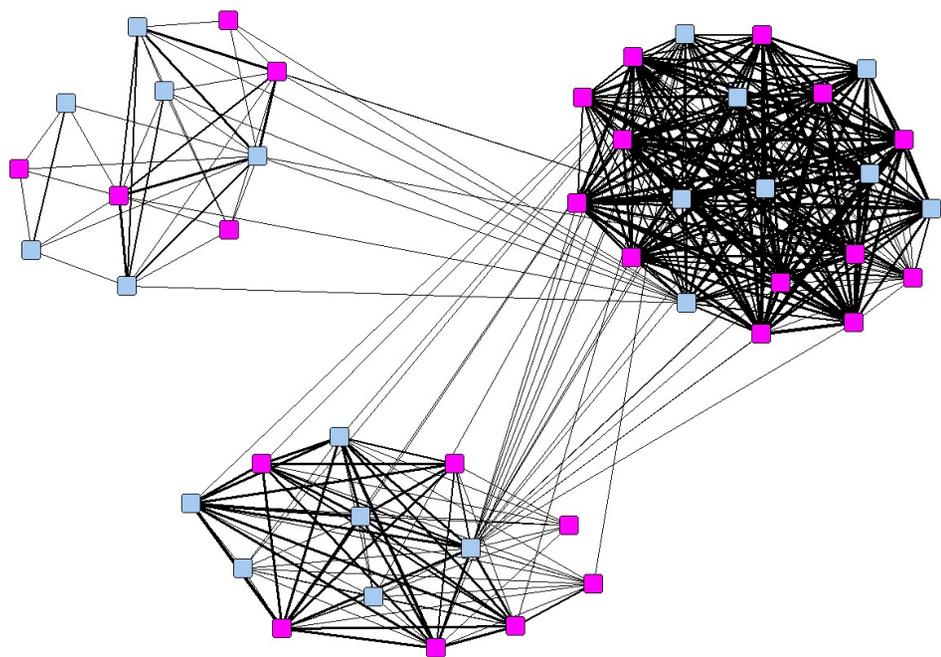
Figure 4. Relationship between SRI association and relatedness, using the Wang (2017) estimator, for male and female *Thyroptera tricolor*. Quadratic assignment procedure regression lines shown with 95% confidence limits.

Figure 5. A) Logistic regression coefficients for assignment of individuals to community as predicted by maximizing modularity. Significance is indicated as \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . B) Average within community relatedness for each sex and species. Standard errors obtained by bootstrapping.

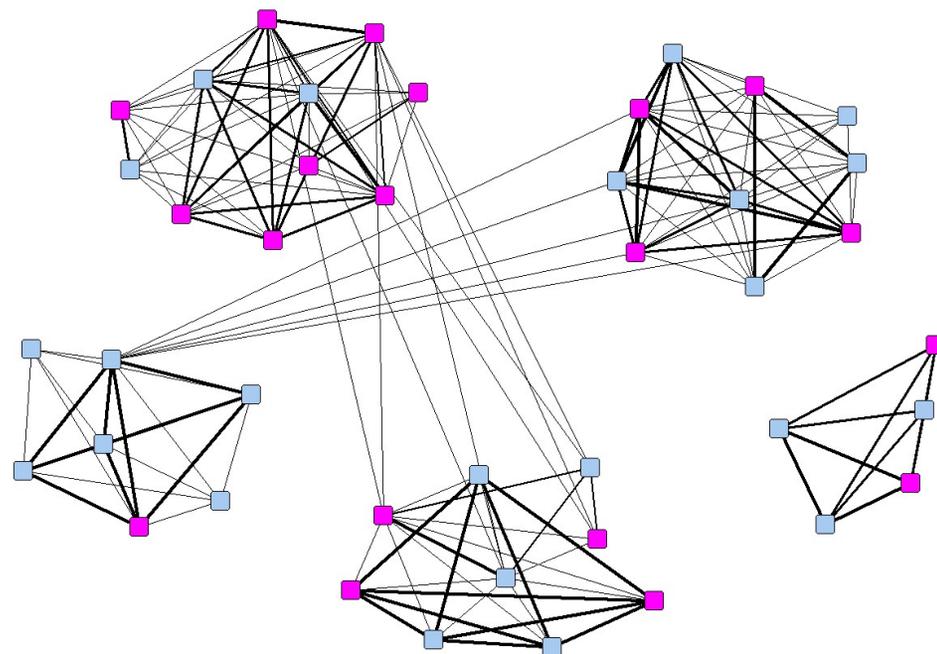
Figure 6. Amount of roost switching, as measured by the number of roosts occupied per bat divided by number of roost observations plotted against A) the regression

coefficient for the relationship between association and relatedness and B) the logistic regression coefficient for assignment of individual to community as defined by maximizing modularity on the basis of relatedness. Females are indicated by black points, males by gray points.

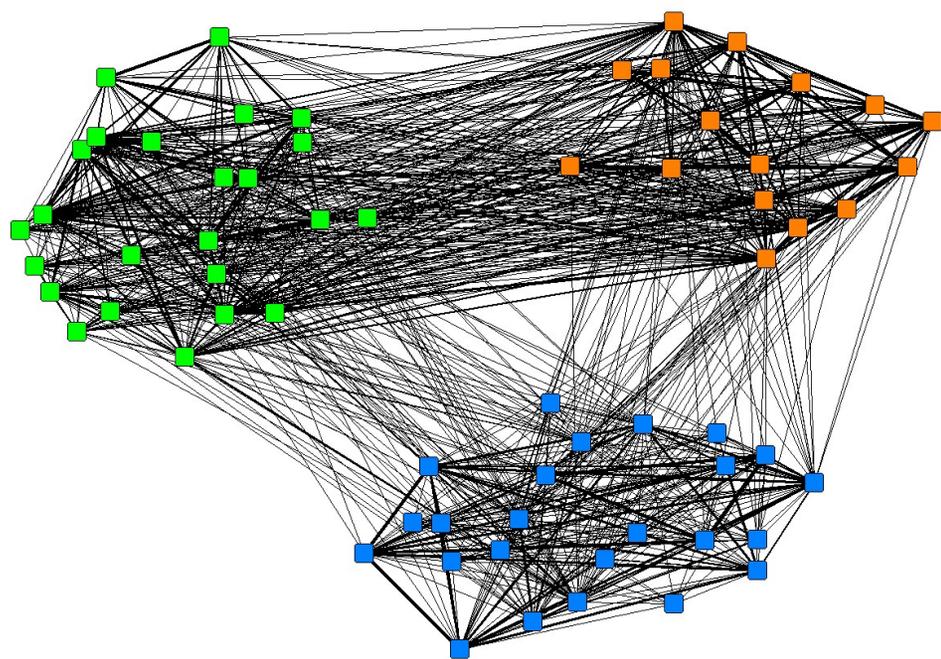
A. *R. naso*



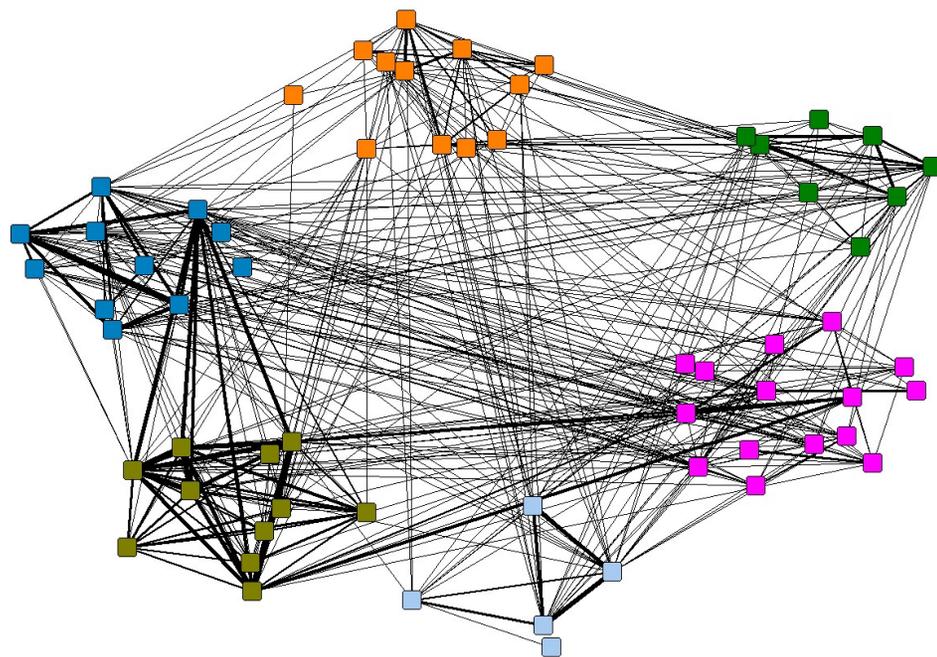
B. *T. tricolor*



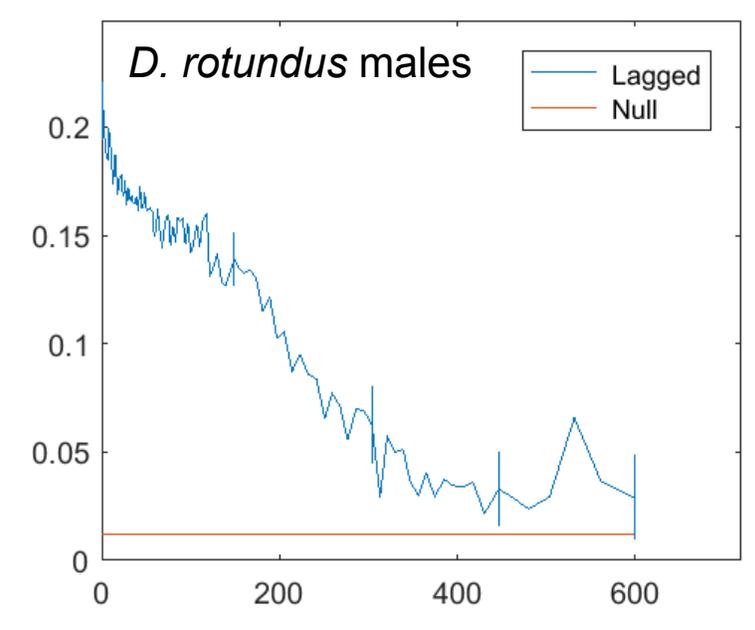
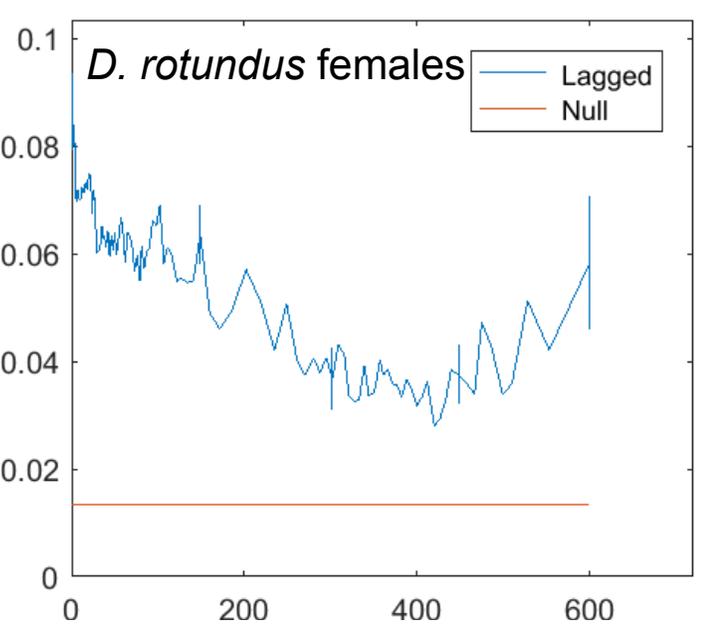
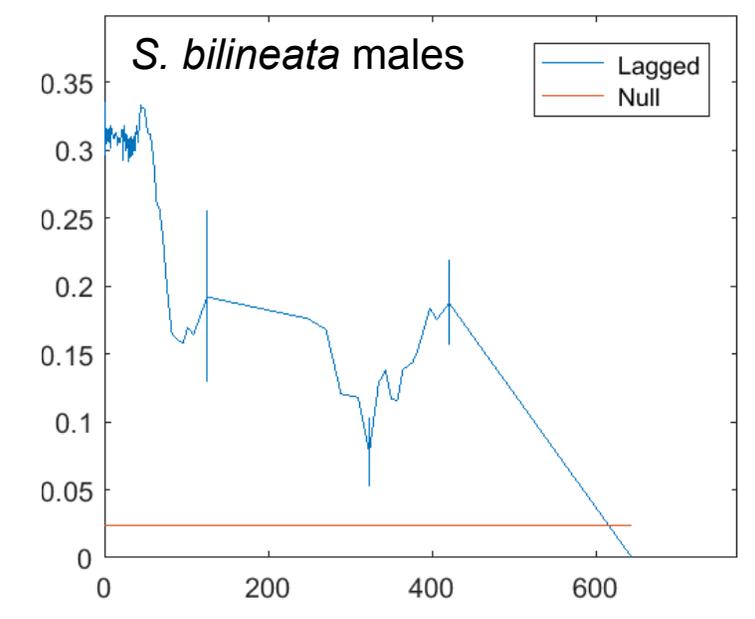
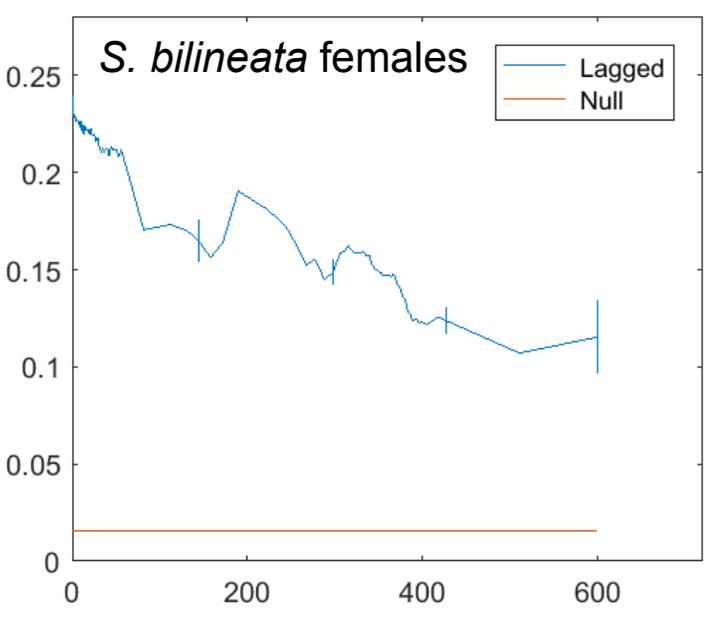
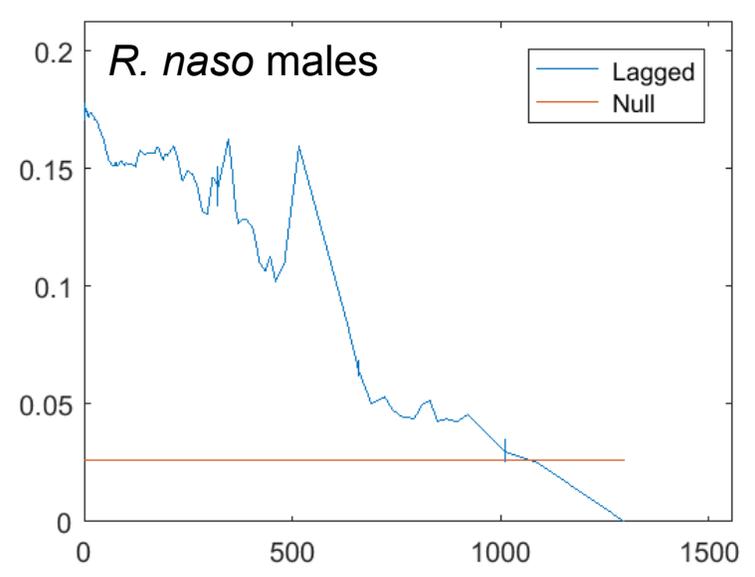
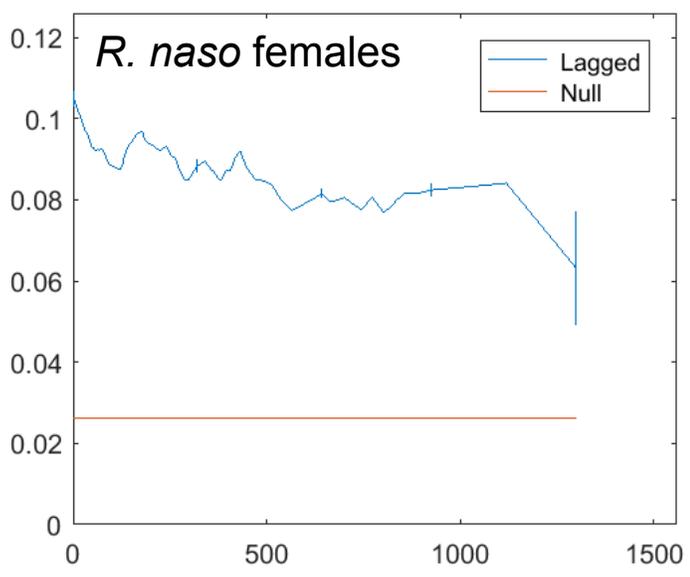
C. *D. rotundus* females



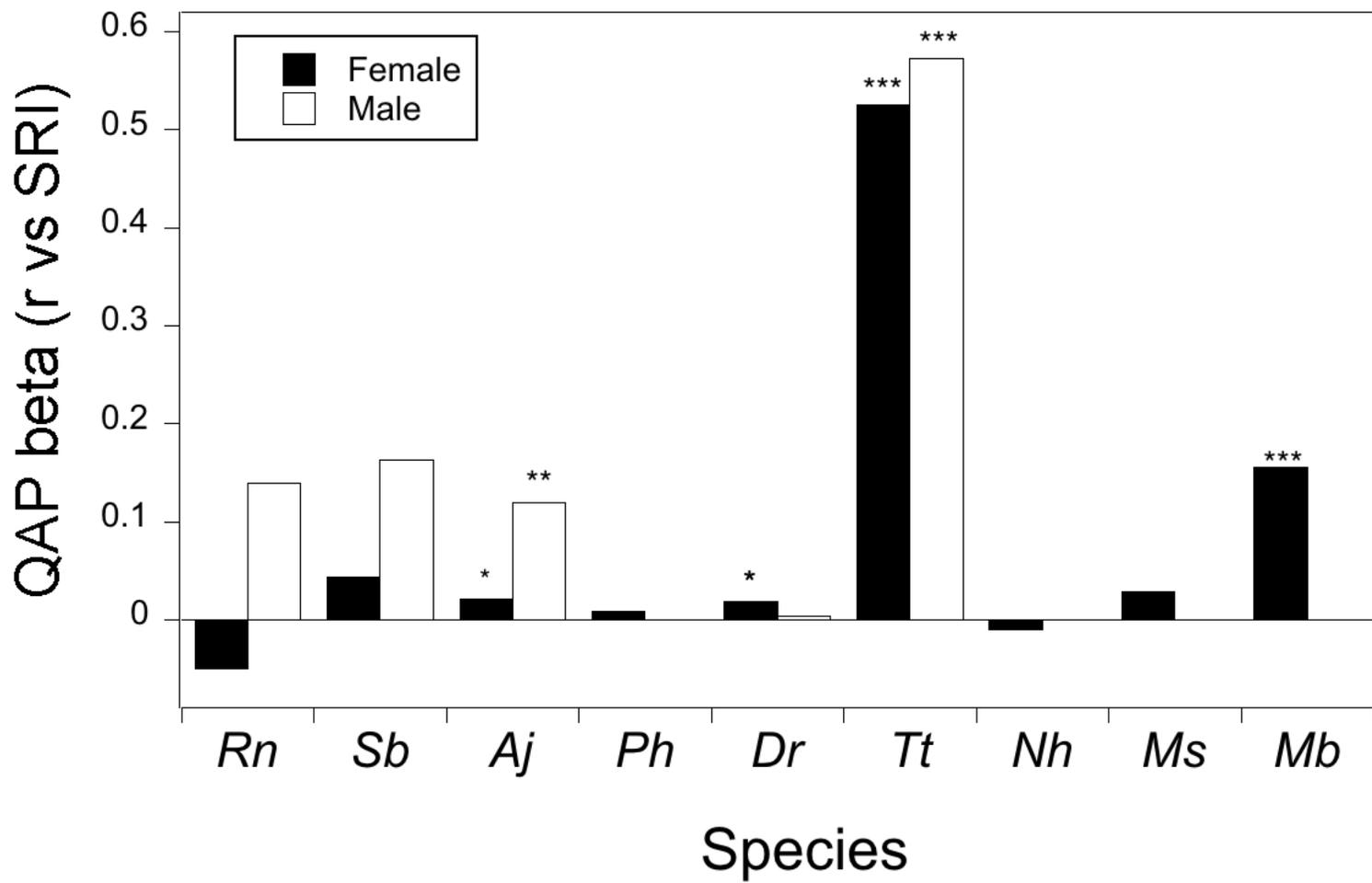
D. *D. rotundus* males



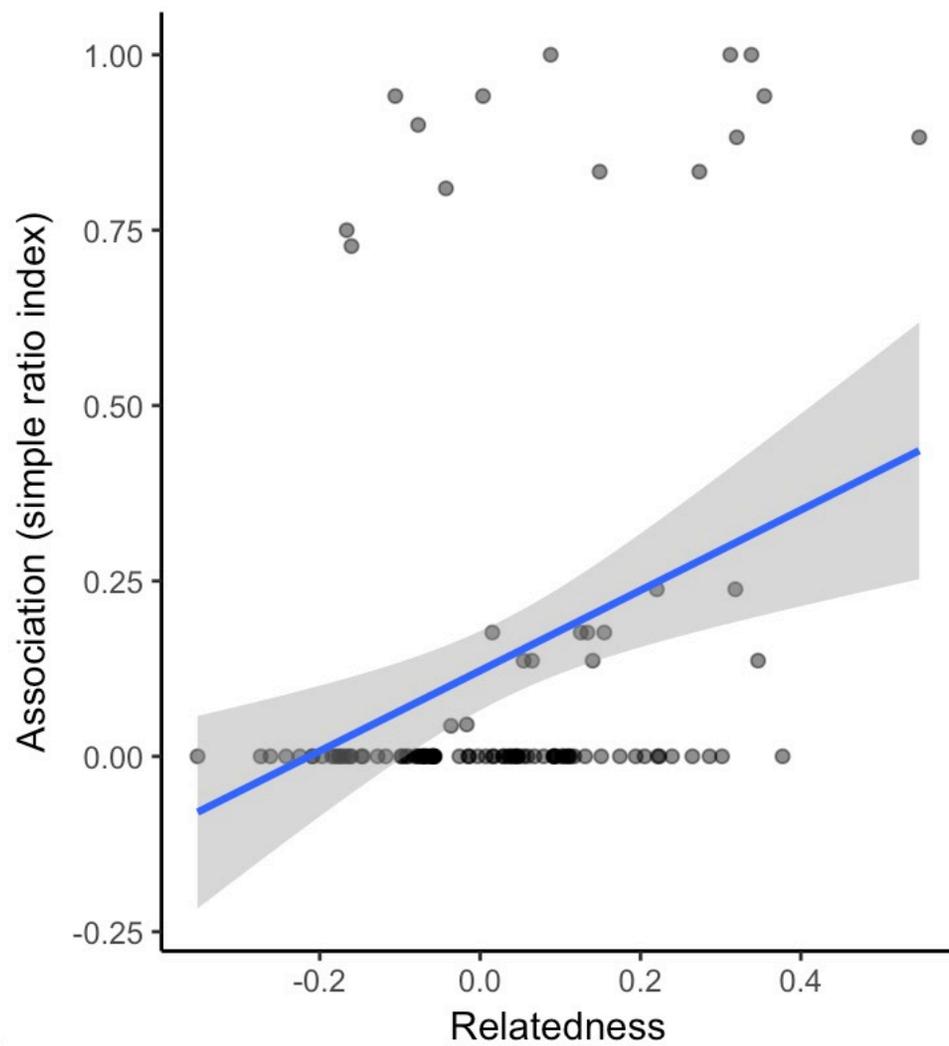
Standardized association rate



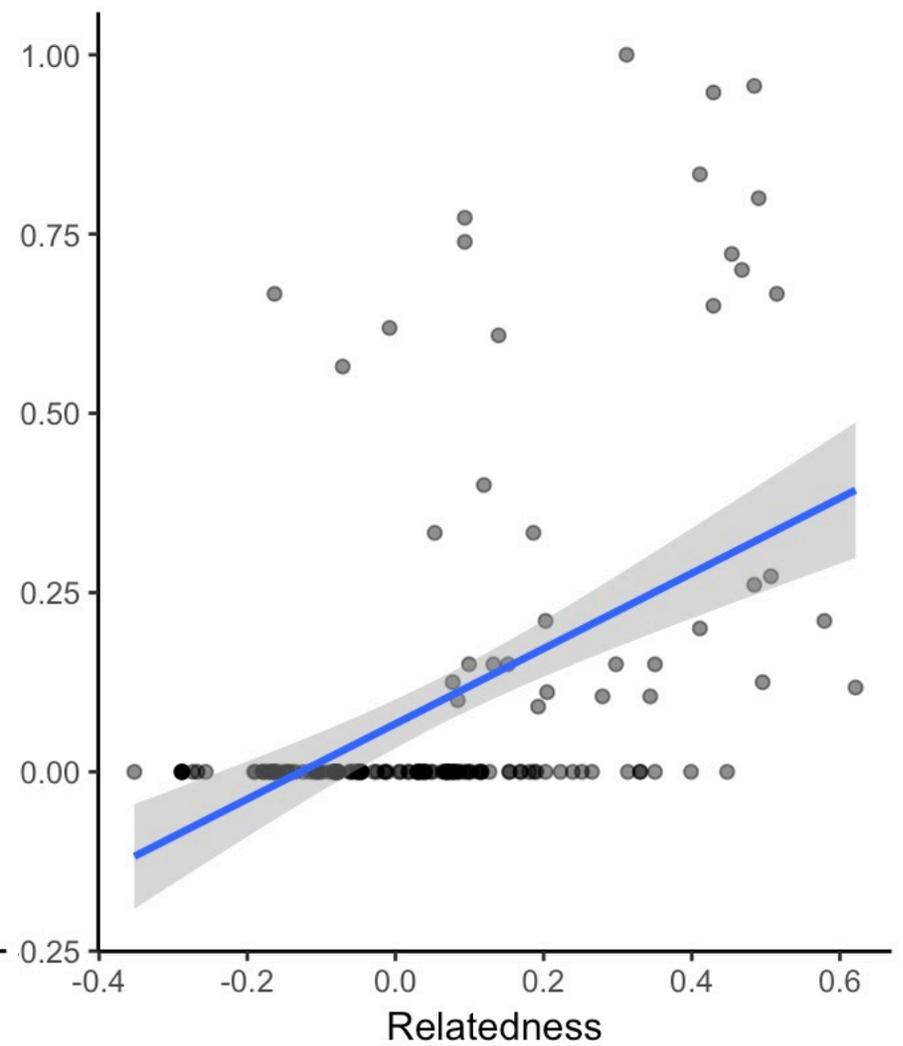
Time lag (days)



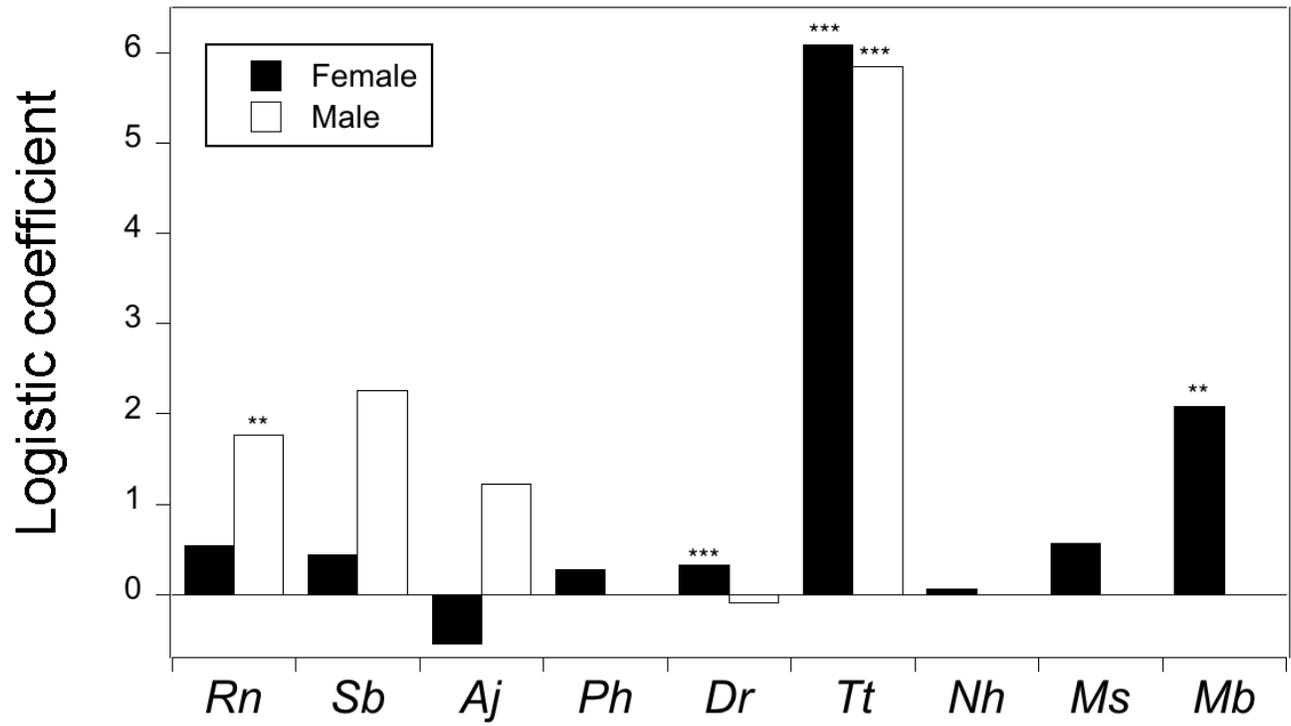
A. Males



B. Females



A.



B.

