

1 **Genetic relatedness cannot explain social bonds in black-and-white ruffed**
2 **lemurs (*Varecia variegata*).**

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20

21 **ABSTRACT**

22 Several primates exhibit fission-fusion social dynamics, yet the factors
23 shaping variable associations among subgroup members have not been widely
24 addressed. Associations may occur simply because of shared habitat preferences;
25 however, social ties may also be influenced by genetic relatedness (kinship) or
26 social attraction. Here, we investigate the association patterns of wild black-and-
27 white ruffed lemurs, *Varecia variegata*, in Ranomafana National Park, Madagascar
28 using behavioural, spatial (home range), and genetic data from twenty-four
29 individually identified animals. We collected 40,840 records of group composition
30 over a 17-month period and from this calculated pairwise association indices. We
31 also used ranging coordinates and genetic samples to estimate patterns of spatial
32 overlap and kinship, and then related these measures to patterns of affiliation using
33 Mantel tests and MRQAP. From these analyses, we found that dyadic ruffed lemur
34 social associations were generally sparse and weak; that home range overlap was
35 minimal; and that average relatedness within the community was low. We found
36 no evidence that kinship was related to patterns of either spatial overlap or social
37 association; instead, associations were primarily driven by space use. While home
38 range overlap explained most of the variation seen in social association, some
39 variation remains unaccounted for, suggesting that other social, ecological, and
40 biological factors such as shared resource defense or communal breeding might
41 also play a role in social attraction among members of this species.

42

43 *Keywords:* social network analysis, range use, spatial overlap, Association Index,
44 kinship, fission-fusion, microsatellites, primates

45

46 **INTRODUCTION**

47 Animal social systems reflect non-random relationships among
48 neighbouring conspecifics, the content, quality, and patterning of which define their
49 social structure (Hinde, 1976). In fact, there is growing evidence that taxa as
50 diverse as fishes, lizards, birds, cetaceans, and equids exhibit social associations
51 that are not only non-random, but highly structured (Augusto, Frasier, &
52 Whitehead, 2017; Croft et al., 2012, 2005; Firth et al., 2017; Spiegel, Sih, Leu, &
53 Bull, 2018; Stanley, Mettke-Hofmann, Hager, & Shultz, 2018). Individuals vary in
54 the numbers, strengths, and stabilities of their social ties (Croft et al., 2005;
55 McDonald, 2007; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006;
56 Silk et al., 2010a; Stanley et al., 2018), as well as in their preferences for social
57 associates (e.g., Cords, 2002; Gero, Gordon, & Whitehead, 2015; Kohn, Meredith,
58 Magdaleno, King, & West, 2015; Mourier, Vercelloni, & Planes, 2012; Perry, 2012;
59 Schülke, Bhagavatula, Vigilant, & Ostner, 2010)—outcomes of which can be
60 evolutionarily significant (Seyfarth & Cheney, 2012; Silk, 2007). For example, the
61 extent and/or strength of females' social connections have been positively linked
62 to higher fertility (*Macaca mulatta*: Brent et al., 2013; humans: Balbo & Barban,
63 2014), longer lifespan (*Papio cynocephalus*: Alberts, 2019; Archie, Tung, Clark,
64 Altmann, & Alberts, 2014; *Papio ursinus*: Silk et al., 2010b), and greater offspring
65 survival (*Equus caballus*: Cameron, Setsaas, & Linklater, 2009; *Papio*

66 *cynocephalus*: Silk, Alberts, & Altmann, 2003; *Papio ursinus*: Cheney, Silk, &
67 Seyfarth, 2016; Silk et al., 2009; *Physeter microcephalus*: Whitehead, 1996).
68 Similarly, males that form strong social bonds have been shown to be more
69 successful at forming coalitions, achieving high rank, and siring more offspring
70 than males with weaker social bonds (e.g., *Chiroxiphia linearis*: McDonald, 2007;
71 *Macaca assamensis*: Schülke et al., 2010; *Pan troglodytes*: Gilby et al., 2013).
72 Nevertheless, while the long-term health and fitness outcomes of social bonds
73 have been the focus of much investigation, the proximate factors shaping social
74 preferences have received comparatively little attention.

75 Several hypotheses have been proposed to explain social preference, the
76 most popular being kinship, whereby group members show preferential
77 associations with and, in the case of kin selection, are more likely to direct costly
78 altruistic behaviours toward close genetic relatives (Hamilton, 1964). For instance,
79 many female mammals exhibit social preferences toward maternal kin (Smith,
80 2014), a pattern observed in primates in particular (reviewed in Langergraber,
81 2012), but also in spotted hyaenas (Wahaj et al., 2004), African elephants (Archie,
82 Moss, & Alberts, 2006), dolphins (Frère et al., 2010), and mountain goats (Godde,
83 Côté, & Réale, 2015), among others. Social preferences toward kin can be driven
84 by the benefits of associating with relatives, such as allomaternal care (reviewed
85 in Briga, Pen, & Wright, 2012; Pope, 2000; and in some cases even brood
86 parasitism, Andersson, 2017), reduced aggression and infanticide risk (reviewed
87 in Brown & Brown, 1996; Agrell, Wolff, & Ylonen, 1998), foraging advantages
88 (Griffiths & Armstrong, 2002; Nystrand, 2007), and shared social and ecological

89 knowledge (McComb, Moss, Durant, Baker, & Sayialel, 2001; Salpeteur et al.,
90 2015). However, social integration has also been shown to have strong direct
91 fitness consequences between nonrelatives (Baden, Wright, Louis, & Bradley,
92 2013; Cameron et al., 2009; G. G. Carter & Wilkinson, 2015; Riehl, 2011),
93 suggesting that social bonds can evolve based on these direct benefits alone.
94 Moreover, evidence for kin-biased relationships in other species, particularly those
95 with higher fission-fusion dynamics, is weak (e.g., Best, Dwyer, Seddon, &
96 Goldizen, 2014; K. D. Carter, Seddon, Frère, Carter, & Goldizen, 2013; Hirsch,
97 Prange, Hauver, & Gehrt, 2013; Langergraber, Mitani, & Vigilant, 2007, 2009;
98 Moscovice et al., 2017; Wilkinson, Carter, Bohn, & Adams, 2016), raising
99 questions as to the ubiquity of kinship in the formation and maintenance of social
100 ties.

101 One complicating factor in determining whether and how kinship shapes
102 social bonds is that it can be difficult to decouple social associations due to kinship
103 from associations due to other social and spatial contexts (reviewed in Doreian &
104 Conti, 2012; Wey, Blumstein, Shen, & Jordán, 2008). For example, in some
105 species it is difficult to differentiate whether strong associations are due to strong
106 genetic ties or to other factors, such as sex or age (Lusseau & Newman, 2004;
107 Mourier et al., 2012), habitat utilization (Wiszniewski, Allen, & Möller, 2009), or
108 foraging specializations (Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes,
109 2012; Gilby & Wrangham, 2008; Griffiths & Armstrong, 2002; Mitani, Merriwether,
110 & Zhang, 2000). Indeed, patterns of social association have been found to
111 correlate with spatial overlap (i.e., overlapping home ranges) more strongly than,

112 or to the exclusion of, kinship in a number of species (Best et al., 2014; K. D. Carter
113 et al., 2013; Frère et al., 2010; Strickland, Gardiner, Schultz, & Frère, 2014).
114 Moreover, although individuals living in closer physical proximity are more prone
115 to interact (e.g., Clutton-Brock, 1989; Kossinets & Watts, 2006), conspecifics with
116 high levels of spatial overlap may also mediate their interactions by temporally
117 modifying range use, such that animals with highly overlapping ranges may
118 interact minimally, if at all (e.g., temporal avoidance) (Leu, Bashford, Kappeler, &
119 Bull, 2010; Ramos-Fernández, Boyer, Aureli, & Vick, 2009; Strickland et al., 2017).
120 While still rare, studies that consider the simultaneous effects of spatial overlap
121 and kinship on association patterns are thus important to understanding the role
122 of social preference in the evolution of social systems and sociality (e.g., Best et
123 al., 2014; K. D. Carter et al., 2013; Frère et al., 2010; Lusseau et al., 2006; Maher,
124 2009; Podgórski, Lusseau, Scandura, Sönnichsen, & Jędrzejewska, 2014;
125 Strickland et al., 2014).

126 Ruffed lemurs (Genus *Varecia*) are moderately-sized frugivores (Baden,
127 Brenneman, & Louis Jr., 2008; Balko & Underwood, 2005) that live in groups
128 (hereafter “communities”) comprising as many as 30 adult and subadult individuals
129 and their offspring (Baden, Webster, & Kamilar, 2016 and references therein).
130 From earlier work, we know that communities exhibit high fission-fusion dynamics,
131 with members varying in their degrees of home range overlap and number and
132 strength of social ties (Baden, 2011; Baden & Gerber, n.d.; Baden et al., 2016;
133 Vasey, 2006). Moreover, studies of microsatellite markers and mitochondrial DNA
134 have shown that while average pairwise relatedness within communities is low

135 (i.e., both sexes disperse: Baden et al., 2014), communities nevertheless contain
136 networks of closely related kin (e.g, Baden, 2011; Baden et al., 2013). Taken
137 together, these lines of evidence suggest that community members may be
138 actively choosing social associates, and that these associations may be shaped
139 by a number of ecological, social, and biological factors. Here, we investigate the
140 relative influences of space use and kinship on the strength of associations
141 amongst members of a black-and-white ruffed lemur (*Varecia variegata*)
142 community. Specifically, we quantify dyadic measures of association, home range
143 overlap, and genetic relatedness to address the overarching question: What
144 influences social association in ruffed lemurs?

145

146 **METHODS**

147 **Study site and subjects**

148 We collected data from one *V. variegata* community at Mangevo [21°220
149 6000 S, 47°280 000 E], a mid-elevation (660-1,200 m) primary rainforest site
150 located in the southeastern parcel of Ranomafana National Park, Madagascar
151 (Wright et al., 2012) during 16 months of study (August–December 2007;
152 February– December 2008). At the time of the study, the community included 24
153 adults and subadults (8 adult females, 11 adult males, 5 subadult males). All
154 individuals in this study were habituated and individually identified via radio-collars
155 or unique collar-tag combinations prior to behavioural observations (see Baden et
156 al., 2016 for specific details). Animals were collared under veterinary supervision
157 following a strict protocol (Glander, 1993). Nineteen infants were born in the 2008

158 birth season and were present from October to December 2008, when the study
159 ended. Sampling efforts resulted in a total of 4,044 focal observation hours.

160

161 **Ethical note**

162 Permission to conduct research was granted by Madagascar's National
163 Parks (ANGAP/MNP, #084/07-041/08), and research protocols were in
164 compliance with Stony Brook University IACUC #2005-20081449. All animal
165 protocols followed the Guidelines for the treatment of animals for teaching and
166 research recommended by ASAB/ABS (2019).

167

168

169 **Data collection**

170 *Behavioural monitoring*

171 We collected data during dawn to dusk follows of focal individuals. We
172 located focal subjects at the beginning of each observation period via radio-
173 telemetry and selected new subjects daily. We never sampled focal subjects on
174 consecutive days and every effort was made to follow all subjects at least once per
175 month. If an individual with a collar-tag was located in association with a radio-
176 collared focal individual prior to 10:00 h, this individual became the new focal
177 subject for that observation period. Observational periods ranged in duration
178 between 8 to 11 hours depending on seasonal differences in day length and time
179 needed to locate animals at dawn.

180 Upon initial contact with the focal individual, we recorded the number and
181 identities of all other individuals present within the subgroup. To do so, one
182 observer remained with the focal individual while the remaining three team
183 members spread out to locate and identify all other members of the subgroup. *A*
184 *priori*, individuals were considered members of a subgroup only if they were within
185 50 m of the group center and were seen associating, traveling with and maintaining
186 proximity to members of the subgroup being followed (see Baden et al., 2016 for
187 details). After initial contact, we monitored subsequent changes in subgroup size,
188 composition (age/sex class, individual identity), and cohesion (i.e., the greatest
189 distance between any two subgroup members), as well as activity state of the focal
190 subject using instantaneous scan sampling techniques collected at 5 min intervals
191 (Altmann, 1974). We recorded a total of 40,840 group scans.

192 We collected simultaneous GPS coordinates at 10-min intervals from as
193 close to the focal individual as possible to document daily individual range use. We
194 recorded spatial coordinates only if estimated positional error was less than 10 m.

195

196 *Genetic sampling*

197 In addition, we collected genetic samples from 38 black-and-white ruffed
198 lemurs from the Mangevo population, including all subjects in this study, during
199 five capture seasons spanning four consecutive years (2005-2008; see Baden,
200 2011 for details). Sample collection occurred under veterinary supervision and
201 followed a strict protocol outlined by Glander (1993). All capture procedures

202 occurred during non-reproductive seasons in the absence of infants and
203 dependent offspring.

204 For each individual captured, one of us (ALB) collected approximately 1
205 ml/kg of whole blood (~4 cc) from the femoral vein and four 2mm tissue biopsies
206 from ear pinnae. All samples were stored in 5ml of lysis buffer solution (0.1 M Tris-
207 HCl pH, 8.0, 0.1 M EDTA, 0.01 M NaCl, and 0.5% w/v SDS) at ambient
208 temperature in the field (7 to 21 days) (Longmire, Gee, Hardekopf, Graham, &
209 Mark, 1992). We then banked samples in a -80°C freezer at the Madagascar
210 Biodiversity Partnership headquarters in Antananarivo, Madagascar and
211 subsequently at the Yale Molecular Anthropology Lab in New Haven, CT until
212 analysis.

213

214 **Data analysis**

215 *Association strength*

216 Sampling was biased toward radio-collared females; we therefore
217 subsampled our data prior to association analyses. Details are presented in Baden
218 et al. (2016), but briefly, we divided our dataset into monthly periods and according
219 to the sex of the focal individual. Using only scans for which all individuals were
220 known, we randomized point scans and selected X scans to include in the dataset
221 for each sex, where X is 90% of the point scans for the sex with the fewest scans
222 in a given month. This procedure resulted in the inclusion of a total of 11,784 point
223 scans, with equal numbers of scans targeting male and female focal subjects in
224 each month (Baden et al., 2016).

225 We used SOCPROG 2.9 (Whitehead, 2009) to calculate association indices
226 between all pairs of individuals using the “simple ratio” index, which quantifies the
227 proportion of time that two individuals are observed together relative to their total
228 observation time overall. This index is appropriate when individuals are equally
229 likely to be correctly identified (Cairns & Schwager, 1987; Ginsberg & Young, 1992;
230 Whitehead, 2008), which is the case for this population. Given that subgroup
231 composition in this community changes approximately every 90 minutes (Baden
232 et al., 2016), we used a 6-hour sampling interval to reduce autocorrelation among
233 periods. We also removed any subject observed in fewer than 10 sampling
234 periods. Our final dataset included 8 adult females and 9 adult males observed in
235 over 11,171 point scans.

236 To examine seasonal variation in associations, we organized the subsetted
237 data from 2008 into three seasons according to female reproductive state as
238 defined by Baden et al. (2013). Using the protocols described above, our final
239 datasets included: 8 females and 9 males over 5,051 scans during the
240 nonbreeding season (January through June); 7 females and 8 males over 3,267
241 scans during the mating/gestation season (July through September); and 8
242 females and 6 males over 2,664 scans during the birth/lactation season (October
243 through December).

244

245 *Spatial overlap*

246 We calculated home range overlap between all pairs of individuals using a
247 utilization distribution overlap index (UDOI; Fieberg & Kochanny, 2005)

248 implemented in the R package *adehabitat* (Calenge, 2011), as described in Baden
249 & Gerber (n.d.). The UDOI is an index of space-use sharing between two utilization
250 distributions (UDs). UDOI values can range from 0 to 1, with a UDOI of 0 indicating
251 no home range overlap and a UDOI of 1 indicating that home ranges are uniformly
252 distributed and have 100% overlap. Values can also be >1 if both UD are
253 nonuniformly distributed and also have a high degree of overlap. Values <1
254 indicate less overlap relative to uniform space, whereas values >1 indicate higher
255 than normal overlap relative to uniform space. We calculated four UDOIs for all
256 pairs of individuals: one annual UDOI, and three seasonal UDOIs according to
257 female reproductive state, as for association analyses described above.

258

259 *Relatedness*

260 We genotyped individuals at a suite of 15 polymorphic microsatellite loci (see
261 Baden, 2011 and Baden et al., 2014 for details). We extracted total genomic DNA
262 from blood and/or tissue samples using standard nucleic acid extraction kits
263 (QIAamp DNA Mini Kit; Qiagen) automated on a QiaCube (Qiagen). Extraction
264 procedures followed the manufacturer's protocols, with the following modification
265 to the tissue extraction procedures: samples were allowed to lyse initially in ASL
266 buffer for 24-48 hours rather than 10 minutes.

267 We carried out PCR amplifications in a total reaction volume of 25 μ l
268 consisting of 2 μ l template, 12.5 μ l Qiagen HotStar Taq Master Mix, and 10 μ M of
269 each primer. Amplification conditions were as follows: initial denaturation at 95 °C
270 for 15 min; 35 cycles of 30 s at 94 °C, 40 s at 54 to 60 °C (see Louis et al., 2005),

271 1 min at 72 °C, and a final extension of 7 min at 72 °C. The 5' end of the forward
272 primer was fluorescently labeled, and amplification products were separated and
273 visualized using capillary electrophoresis (ABI 3730xl Genetic Analyzer). We
274 assessed allele sizes relative to an internal size standard (ROX-500) using Gene
275 Mapper software (Applied Biosystems), and scored final genotypes based on
276 multiple independent reactions (Taberlet, 1996). Panels yielded PIsib (Queller &
277 Goodnight, 1989) values of 2.7×10^{-5} , demonstrating the very low probability that
278 two individuals would share the same multilocus genotype by chance. We further
279 tested the robusticity of this suite of loci for estimating relatedness with a
280 rarefaction analysis as in Altmann & Alberts (1996) and de Ruiter & Geffen (1998)
281 using the program RE-RAT (<http://people.musc.edu/~schwach/>). We estimated
282 pairwise relatedness among individuals (r) following Queller & Goodnight (1989) using
283 the program GenAlEx 6.5 (Peakall & Smouse, 2012). Relatedness was based on allele
284 frequencies derived from a larger population of 38 adult multilocus genotypes (Baden,
285 2011). Fine scale dyadic relatedness assessments (e.g., distinguishing between
286 full and half-sibs) are not possible in most microsatellite studies, and in fact, the
287 ability to differentiate relatedness disjunctions on such a scale would probably
288 require 30 to 60 microsatellite loci (Stone & Björklund, 2001). We therefore
289 consider “related dyads” to be those with r -values ≥ 0.25 ; we made no attempt to
290 further distinguish categories or degrees of relatedness.

291

292 *Correlations among association strengths, spatial overlap, and relatedness*

293 We used Mantel tests to examine whether association indices were related
294 to either spatial overlap or relatedness, as well as test for a correlation between
295 spatial overlap and relatedness (Mantel, 1967). We further used a multiple
296 regression quadratic assignment procedure (MRQAP; Dekker, Krackhardt, &
297 Snijders, 2007) to determine relationships between the response variable—
298 association index—and predictor variables—sex, spatial overlap, and relatedness.
299 For sex, we used a matrix of sex similarity, which used values of 1 (same sex) and
300 0 (different sex). MRQAP tests each pairwise combination of response and
301 predictor matrices while holding the remaining predictor matrices constant. We
302 performed both Mantel tests and MRQAP for the overall dataset as well as in each
303 of the three seasons using SOCPROG 2.9 (Whitehead, 2009).

304

305 *Quantifying relatedness among dyads with “preferred” association strengths or*
306 *spatial overlap*

307 In addition to the correlations described above, we further investigated
308 patterns of kinship among individuals identified as “preferred” associates (AIs) and
309 those with “preferred” spatial overlap (UDOIs) following methods described in
310 Frère et al. (2010) and Carter et al. (2013). We first divided relationships into
311 “preferred” (>95th percentile of association indices or UDOIs) and “non-preferred”
312 (<=95th percentile). Note that the descriptor “preferred” is clear for associates
313 (dyads observed together more often than others), but dyads with high spatial
314 overlap were not necessarily utilizing shared ranges in coordinated ways. Unlike
315 Frère et al. (2010) and Carter et al. (2013), we did not include an ‘avoided’ category

316 because the number of dyads that did not associate and/or overlap spatially
317 exceed the 5th percentile, which was used as a threshold in previous studies. We
318 then calculated mean observed relatedness for each of the two categories
319 (“preferred” and “non-preferred”) for both AI and UDOI datasets. Next, we
320 randomly resampled relatedness values with replacement for each of the two
321 datasets, using the sample sizes for each category in the empirical data (i.e.,
322 sample sizes for “preferred” and “nonpreferred” were held constant). We repeated
323 this procedure 10,000 times to generate a distribution, and then calculated
324 significance as the fraction of replicates (out of 10,000) in which relatedness of
325 “preferred” AI or UDOI was greater than the observed, empirical value. The script
326 in which we implemented this procedure is available at
327 https://github.com/thw17/Varecia_social_preferences.

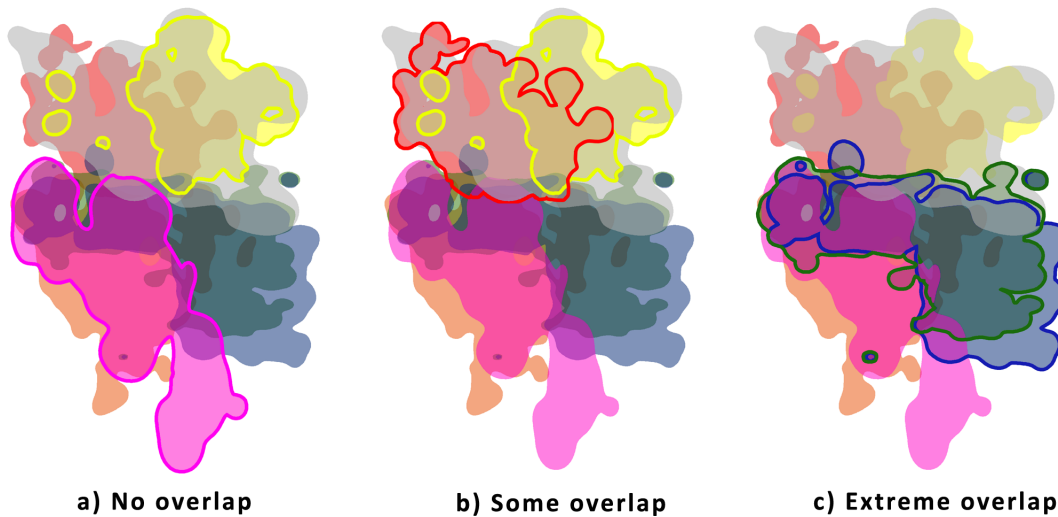
328

329 **RESULTS**

330 *Association strength and spatial overlap*

331 The average overall association index (AI) was 0.05 ± 0.03 (Baden et al.,
332 2016). We observed similar mean AIs in each of the three reproductive seasons
333 (nonbreeding = 0.04 ± 0.02 ; mating/gestation = 0.06 ± 0.03 ; birth/lactation = 0.07
334 ± 0.03). Within seasons, however, individuals varied substantially in their AIs.
335 Average individual AIs varied from 0.01 to 0.11 (nonbreeding = 0.01-0.08;
336 mating/gestation = 0.01-0.11; birth/lactation = 0.01-0.10), while maximum
337 individual AIs ranged from 0.07 to 0.82 (nonbreeding = 0.08-0.82; mating/gestation
338 = 0.07-0.79; birth/lactation = 0.08-0.82).

339 Average home range overlap (UDOI) was 0.211 ± 0.357 . Some dyads did
340 not overlap at all (UDOI = 0), while the maximum UDOI observed was 1.895
341 (Figure 1). As with AIs, we observed similar mean UDOIs in each of the three
342 reproductive seasons (nonbreeding = 0.17 ± 0.27 ; mating/gestation = 0.15 ± 0.29 ;
343 birth/lactation = 0.20 ± 0.43 ; Table 1)



345 *Figure 1. Examples of home range overlap among pairs of individuals within the Mangevo ruffed lemur*
346 *community: a) Females Pink-Yellow and Radio-Yellow have no spatial overlap among home ranges (i.e.,*
347 *UDOI = 0.00), whereas b) females Radio-Yellow and Radio-Red and c) females Radio-Blue and Radio-Green*
348 *share some (UDOI = 0.106) to nearly complete home range overlap (UDOI = 0.951), respectively.*

349

350

351 Table 1. Summary of association indices, utilization distribution overlap indices
352 (UDOIs), and relatedness overall and by reproductive season.

353

Association Indices	n	Mean	SD	Min	Max
Overall	136	0.05	0.03	0.00	0.80
Nonreproductive	136	0.04	0.12	0.00	0.82
Mating/Gestation	105	0.06	0.13	0.00	0.79
Birth/Lactation	91	0.07	0.15	0.00	0.82
UDOIs	n	Mean	SD	Min	Max
Overall	136	0.21	0.36	0.00	1.90
Nonreproductive	136	0.17	0.27	0.00	1.97
Mating/Gestation	120	0.15	0.29	0.00	1.74
Birth/Lactation	78	0.20	0.43	0.00	2.13
Relatedness	n	Mean	SD	Min	Max
Overall	171	-0.06	0.02	-0.72	0.65
Female-female	45	-0.13	0.04	-0.60	0.52
Female-male	90	-0.15	0.02	-0.72	0.28
Male-male	36	-0.13	0.04	-0.54	0.60

354

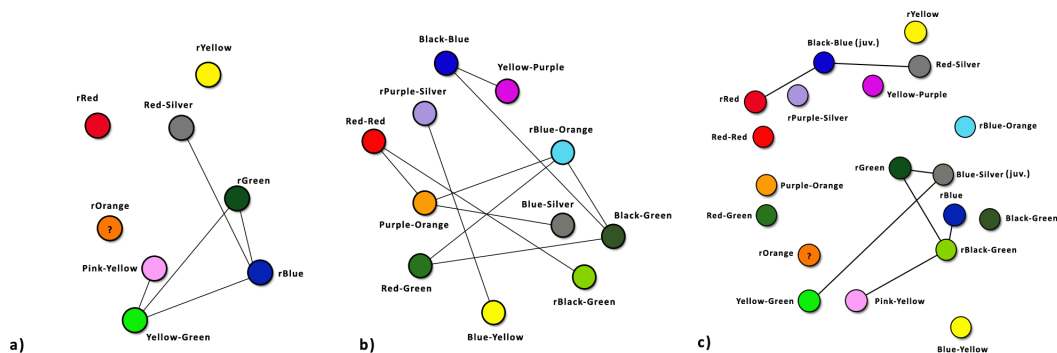
355

356 *Relatedness*

357 Genotypes were 93% complete; all subjects (n = 38) were scored for at least
358 12 loci (average = 14, range = 12 to 15). Allelic richness was 4.33 and average
359 observed heterozygosity was 0.400. There were no significant deviations from
360 Hardy-Weinberg Equilibrium for any of the loci examined, nor was there evidence
361 of null alleles.

362 Results of the rarefaction curve ($y = 0.7991$, $r^2 = 0.9992$) showed average
363 relatedness values stabilizing after 5 loci, with the difference between mean
364 relatedness using 5 and 6 loci changing by only 0.95% (0.023), and the difference
365 between using 6 and 7 loci changing by only 0.56% (0.016). Thus, subsequent

366 dyadic r -value calculations included all possible dyads ($n = 703$ dyads), as all
367 individuals could be compared at 5 or more loci. Average pairwise relatedness
368 among adults within the community was -0.06 ± 0.02 and ranged from -0.72 to
369 0.65 (Table 1; Figure 2).



370

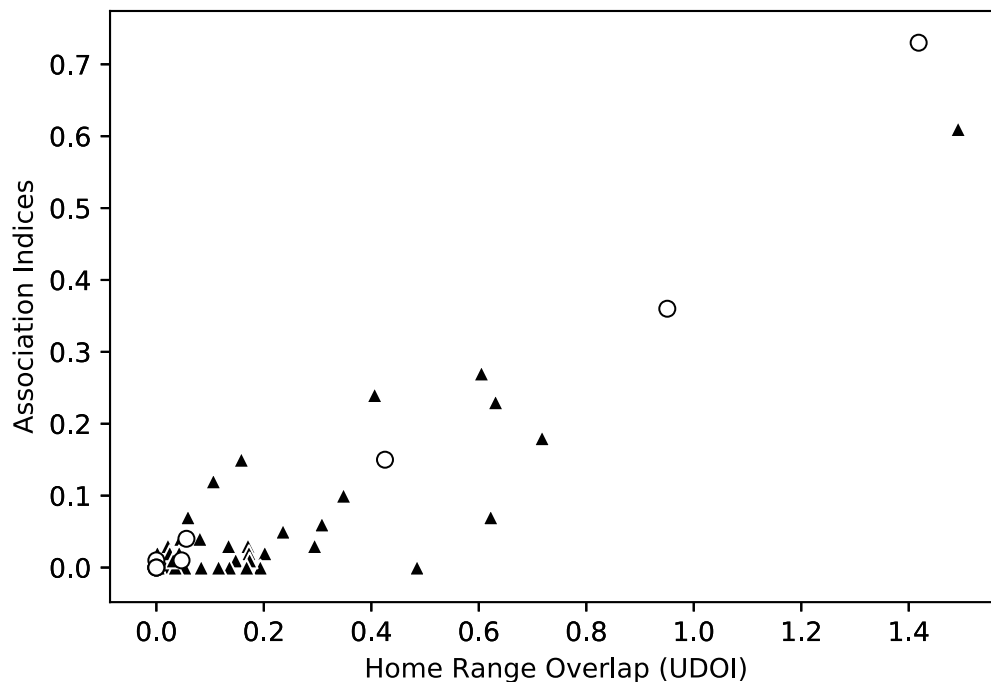
371 *Figure 2. Pairwise genetic relatedness ($r \geq 0.25$) among a) female-female dyads, b) male-male dyads, and*
372 *c) female-male dyads within the Mangevo social community. “?” indicates individuals for which genotype data*
373 *are unavailable. Nodes are organized according to individual home range centroids.*

374

375 *Relationships between association strength, spatial overlap, and relatedness*

376 Using the full dataset, Mantel tests revealed that kinship was unrelated to
377 either home range overlap (UDOI; $n = 25$, $r = 0.047$, $p = 0.724$) or association
378 indices (AI; $n = 14$, $r = 0.120$, $p = 0.294$), whereas UDOI and AI were significantly
379 correlated ($n = 17$, $r = 0.789$, $p \ll 0.001$; Figure 3). This pattern held across all
380 three reproductive seasons (Table 2). It is worth noting, however, that the
381 correlation coefficient between UDOI and AI in the nonbreeding season was much
382 lower, albeit still significantly positive, than the mating/gestation and birth/lactation
383 seasons, which were very similar (Table 2). Similarly, when we used MRQAPs to
384 jointly analyze the effects of UDOI, kinship, and sex on AI, in every time period we
385 analyzed, the partial correlations between UDOI and AI were always significantly

386 positive, while kinship and sex were never significantly correlated with AI (Table
387 3).



388

389 *Figure 3. Scatterplot illustrating the relationship between social association (AI) and home range overlap*
390 *(UDOI). AIs range from 0 (no association) to 1 (100% association). Similarly, UDUIs range from 0 (no overlap)*
391 *to 1 (complete overlap); values of >1 are possible if both UDUs are nonuniformly distributed and also have a*
392 *high degree of overlap. Values <1 indicate less overlap relative to uniform space, whereas values >1 indicate*
393 *higher than normal overlap relative to uniform space. White circles indicate kin ($r \geq 0.25$); black triangles*
394 *indicate non-kin ($r < 0.25$).*

395

396

397 Table 2. Results from Mantel tests correlating Association Indices with utilization
398 distribution overlap indices (UDOIs), and relatedness overall and by reproductive
399 season.

400

Season	Variable	Records	N	Correlation	<i>p</i> -value
Overall	UDOI	11,171	17	0.789	<<0.001
Overall	Relatedness	11,171	14	0.120	0.294
Mating	UDOI	3,267	13	0.891	<<0.001
Mating	Relatedness	3,267	13	0.099	0.392
Nonbreeding	UDOI	5,051	14	0.566	<<0.001
Nonbreeding	Relatedness	5,051	14	0.149	0.184
Birth/gestation	UDOI	2,664	11	0.892	<<0.001
Birth/gestation	Relatedness	2,664	11	0.159	0.254

401 Note: Overall includes 2007-2008, whereas seasonal measures are from 2008
402 only. N indicates the number of individuals included in each analysis; individuals
403 had to be represented in both datasets in order to be included in the analyses for
404 a given season.

405
406

407

408 Table 3. Results from a multiple regression quadratic assignment procedure (MRQAP) investigating the partial relationships
 409 of association (AI) with utilization distribution overlap indices (UDOI), relatedness, and sex.

Season	N	UDOI		Relatedness		Sex	
		Partial corr	<i>p</i> -value	Partial corr	<i>p</i> -value	Partial corr	<i>p</i> -value
Overall	14	0.920	<<0.001	0.035	0.754	0.056	0.617
Nonbreeding	11	0.655	<<0.001	0.123	0.356	-0.113	0.460
Mating/gestation	10	0.873	<<0.001	-0.049	0.742	0.281	0.720
Birth/lactation	8	0.941	<<0.001	0.296	0.144	0.102	0.530

410

411

412 *Relatedness among dyads with “preferred” association strengths or spatial overlap*

413 Average relatedness among “preferred” dyads, defined as falling in the
414 >95th percentile of AIs (5 of 91 dyads), was significantly higher than among dyads
415 classified as “not preferred” (mean $R_{xAI_preferred} = 0.109$ versus mean $R_{xAI_non-preferred}$
416 $= -0.095$; $p = 0.049$). In contrast, average relatedness of dyads with the greatest
417 home range overlap, defined as falling in the >95th percentile of UDOI (10 of 190
418 dyads), was not statistically different from other dyads (mean $R_{xUDOI_preferred} = -$
419 0.015326 versus mean $R_{xUDOI_non-preferred} = -0.03464$, $p = 0.3978$).

420

421 **Discussion**

422 Results from this study illustrate complex relationships among social
423 association, space use, and kinship in wild black-and-white ruffed lemurs, patterns
424 that—while unusual for primates—are well aligned with much of the broader
425 mammalian literature. We found that ruffed lemur social associations varied
426 immensely, ranging from no association between some individuals to dyads
427 observed together more than 75% of the time. From a community perspective, the
428 social network was sparse, with weak associations (AIs) being common. Similarly,
429 home range overlap was minimal and average relatedness among community
430 members was low. These patterns were consistent throughout the year and across
431 reproductive seasons. Together, these and earlier lines of evidence (e.g., Baden,
432 2011; Baden et al., 2016) can be used to characterize ruffed lemurs as having a

433 spatiotemporally dispersed fission-fusion social organization with weak social and
434 kinship ties.

435 Kin selection theory (Hamilton, 1964) has long been invoked to explain the
436 social preferences observed among mammals (e.g., Archie et al., 2006; Frère et
437 al., 2010; Godde et al., 2015; Smith, 2014; Wahaj et al., 2004), particularly in
438 primates (reviewed in Langergraber, 2012; Silk, 2002). In this study, however, we
439 found no evidence that kinship structured either spatial overlap or social
440 association overall in the community. There were exceptions, however, as some,
441 but not all, of the very closest social relationships were between closely related
442 individuals. The closest social ties in the community appear to occur primarily
443 between females and their preferred (often unrelated male) social partners,
444 followed by mothers and their pre-dispersal-aged subadult and adult offspring.
445 Nevertheless, although fewer than ten percent (8.8%) of adults within the
446 community were genetic relatives, nearly three-quarters of adult females (71%)
447 and all of adult males (100%) were closely related to at least one, and up to as
448 many as three other same-sex relative(s) within the community. Thus, while overall
449 patterns of dyadic relatedness suggest that ruffed lemur communities are
450 composed of both kin and non-kin, and that preferred associates are sometimes
451 close relatives, related dyads are not forming spatial networks of kin within the
452 larger communal range. These patterns contrast with the spatially structured
453 matrilineal communities described in *Microcebus murinus* (Eberle & Kappeler, 2006; Radespiel,
454 Lutermann, Schmelting, Bruford, & Zimmermann, 2003), another communally
455 breeding strepsirrhine. Some authors have used this model to hypothesize that, at

456 least in part, kin networks have facilitated the evolution of cooperative infant care
457 (Eberle & Kappeler, 2006). That kin networks don't exist in ruffed lemurs, who also
458 engage in cooperative infant care (Baden et al., 2013), further highlights the
459 uniqueness of their communal breeding strategies.

460 These results build on growing evidence that spatial overlap is more
461 strongly associated with social association than kinship in many taxa characterized
462 by high fission-fusion dynamics (Best et al., 2014; K. D. Carter et al., 2013; Frère
463 et al., 2010; Strickland et al., 2014). Importantly, not all dyads with a high degree
464 of home range overlap were close social associates. Indeed, many dyads with
465 nonzero spatial overlap were never observed together. Similar patterns have been
466 observed in dolphins, giraffes, and water dragons, wherein subjects did not
467 associate, despite sharing complete or near complete home range overlap (i.e.,
468 'social avoidance' in dolphins: Frère et al., 2010; giraffes: K. D. Carter et al., 2013;
469 water dragons: Strickland et al., 2014). Thus, spatial overlap does not necessitate
470 social association. Instead, these results raise important questions related to
471 causation. What motivates social association? Are individuals that bias their time
472 toward overlapping areas simply more likely to associate? Or, in cases where
473 patterns of spatial overlap and social association do not align, is there some
474 additional force shaping these spatial and social decisions? Evaluating these
475 alternatives requires further investigation.

476 Moreover, while home range overlap explained most of the variation seen
477 in social association in ruffed lemurs, some variation remains unaccounted for,
478 suggesting that other social, ecological, and biological factors must also be at play.

479 One possibility is that even weak or infrequent social associations may facilitate
480 cooperative resource defense against other frugivorous competitors. For instance,
481 ruffed lemurs actively defend fruit-bearing trees against larger brown lemur (Genus
482 *Eulemur*) groups for days or even weeks during the resource scarce austral winter
483 (Baden, personal observation). Perhaps social association during these times
484 better equips otherwise solitary individuals to defend valuable fruit resources
485 against interspecific competitors. If this was the case, one might expect higher Als
486 during resource scarce seasons, periods that correspond primarily with
487 mating/gestation, but also birth/lactation seasons. Als were lowest in the
488 nonbreeding, resource abundant periods, though not significantly so, lending
489 minimal support for this hypothesis. In addition, communal breeding plays an
490 important role in female reproductive success in this species (Baden et al., 2013)
491 and might also be important in driving social preferences. For instance, recent work
492 suggests social networks in guppies may be structured by the propensity for non-
493 kin to cooperate (Croft et al., 2009), which could lead to the maintenance of
494 cooperation in the absence of kin assortment (Fletcher & Doebeli, 2009). These
495 lines of research offer exciting opportunities to better understand the myriad factors
496 shaping social preferences in fission-fusion species.

497

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514

515 **References**

- 516 Agrell, J., Wolff, J. O., & Ylonen, H. (1998). Counter-strategies to infanticide in
517 mammals: costs and consequences. *Oikos*, 83, 507–517.
- 518 Alberts, S. C. (2019). Social influences on survival and reproduction: Insights
519 from a long-term study of wild baboons. *Journal of Animal Ecology*, 88(1),
520 47–66. <https://doi.org/10.1111/1365-2656.12887>
- 521 Altmann, J. (1974). Observational Study of Behavior: Sampling Methods.
522 *Behaviour*, 49(3), 227–267. <https://doi.org/10.1163/156853974X00534>
- 523 Altmann, J., & Alberts, S. (1996). Behavior predicts genes structure in a wild
524 primate group. *Proceedings of the National Academy of Sciences of the*
525 *United States of America*, 93(June), 5797–5801. Retrieved from
526 <http://www.pnas.org/content/93/12/5797.short>
- 527 Andersson, M. (2017). Helping relatives survive and reproduce: inclusive fitness
528 and reproductive value in brood parasitism. *American Naturalist*, 189(2),
529 138–152. <https://doi.org/10.1086/689991>
- 530 Archie, E. A., Moss, C. J., & Alberts, S. C. (2006). The ties that bind: genetic
531 relatedness predicts the fission and fusion of social groups in wild African
532 elephants. *Proceeding of the Royal Society B*.
533 <https://doi.org/10.1098/rspb.2005.3361>

- 534 Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social
535 affiliation matters: Both same-sex and opposite-sex relationships predict
536 survival in wild female baboons. *Proceedings of the Royal Society B:
537 Biological Sciences*, 281(1793). <https://doi.org/10.1098/rspb.2014.1261>
- 538 Augusto, J. F., Frasier, T. R., & Whitehead, H. (2017). Social structure of long-
539 finned pilot whales (*Globicephala melas*) off northern Cape Breton Island,
540 Nova Scotia. *Behaviour*, 154(5), 509–540.
541 <https://doi.org/10.1163/1568539X-00003432>
- 542 Baden, A. L. (2011). *Communal infant care in black-and-white ruffed lemurs*
543 (*Varecia variegata*). *Ph.D Thesis*. Stony Brook University.
- 544 Baden, A. L., Brenneman, R. A., & Louis Jr., E. E. (2008). Morphometries of wild
545 black-and-white ruffed lemurs [*Varecia variegata*; Kerr, 1792]. *American
546 Journal of Primatology*, 70(10). <https://doi.org/10.1002/ajp.20583>
- 547 Baden, A. L., & Gerber, B. D. (n.d.). Spatial ecology of black-and-white ruffed
548 lemurs (*Varecia variegata*) in southeastern Madagascar. *American Journal
549 of Primatology*.
- 550 Baden, A. L., Holmes, S. M., Johnson, S. E., Engberg, S. E., Louis, E. E., &
551 Bradley, B. J. (2014). Species-level view of population structure and gene
552 flow for a critically endangered primate (*Varecia variegata*). *Ecology and
553 Evolution*, 4(13). <https://doi.org/10.1002/ece3.1119>
- 554 Baden, A. L., Webster, T. H., & Kamilar, J. M. (2016). Resource seasonality and
555 reproduction predict fission-fusion dynamics in black-and-white ruffed lemurs
556 (*Varecia variegata*). *American Journal of Primatology*, 78(2), 256–279.
557 <https://doi.org/10.1002/ajp.22507>
- 558 Baden, A. L., Wright, P. C., Louis, E. E., & Bradley, B. J. (2013). Communal
559 nesting, kinship, and maternal success in a social primate. *Behavioral
560 Ecology and Sociobiology*, 67(12), 1939–1950.
561 <https://doi.org/10.1007/s00265-013-1601-y>
- 562 Balbo, N., & Barban, N. (2014). Does fertility behavior spread among friends?
563 *American Sociological Review*, 79(3), 412–431.
564 <https://doi.org/10.1177/0003122414531596>
- 565 Balko, E. A., & Underwood, H. B. (2005). Effects of forest structure and
566 composition on food availability for *Varecia variegata* at Ranomafana
567 National Park, Madagascar. *American Journal of Primatology*, 66(1), 45–70.
568 <https://doi.org/10.1002/ajp.20127>
- 569 Best, E. C., Dwyer, R. G., Seddon, J. M., & Goldizen, A. W. (2014). Associations
570 are more strongly correlated with space use than kinship in female eastern
571 grey kangaroos. *Animal Behaviour*, 89, 1–10.
572 <https://doi.org/10.1016/j.anbehav.2013.12.011>
- 573 Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-
574 Lambides, A., Robinson, A. G., ... Platt, M. L. (2013). Genetic origins of
575 social networks in rhesus macaques. *Scientific Reports*, 3, 1–8.
576 <https://doi.org/10.1038/srep01042>
- 577 Briga, M., Pen, I., & Wright, J. (2012). Care for kin: Within-group relatedness and
578 allomaternal care are positively correlated and conserved throughout the
579 mammalian phylogeny. *Biology Letters*, 8(4), 533–536.

- 580 <https://doi.org/10.1098/rsbl.2012.0159>
- 581 Brown, G. E., & Brown, J. A. (1996). Does kin-biased territorial behavior increase
582 kin-biased foraging in juvenile salmonids? *Behavioral Ecology*, 7(1), 24–29.
583 <https://doi.org/10.1093/beheco/7.1.24>
- 584 Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices.
585 *Animal Behaviour*, 35(5), 1454–1469. [https://doi.org/10.1016/S0003-3472\(87\)80018-0](https://doi.org/10.1016/S0003-3472(87)80018-0)
- 586
- 587 Calenge, C. (2011). Home range estimation in R : the adehabitatHR package. *R*
588 *Package*, 1–60. Retrieved from [http://cran.r-](http://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf)
589 [project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf](http://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf)
- 590 Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between
591 unrelated females increase reproductive success in feral horses.
592 *Proceedings of the National Academy of Sciences of the United States of*
593 *America*, 106(33), 13850–13853. <https://doi.org/10.1073/pnas.0900639106>
- 594 Carter, G. G., & Wilkinson, G. S. (2015). Social benefits of non-kin food sharing
595 by female vampire bats. *Proceedings of the Royal Society B: Biological*
596 *Sciences*, 282(1819). <https://doi.org/10.1098/rspb.2015.2524>
- 597 Carter, K. D., Seddon, J. M., Frère, C. H., Carter, J. K., & Goldizen, A. W. (2013).
598 Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial
599 overlap and individual social preferences. *Animal Behaviour*, 85(2), 385–
600 394. <https://doi.org/10.1016/j.anbehav.2012.11.011>
- 601 Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2016). Network connections, dyadic
602 bonds and fitness in wild female baboons. *Royal Society Open Science*,
603 3(7). <https://doi.org/10.1098/rsos.160255>
- 604 Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the*
605 *Royal Society of London. Series B. Biological Sciences*, 236(1285), 339–
606 372. <https://doi.org/10.1098/rspb.1989.0027>
- 607 Cords, M. (2002). Friendship among adult female blue monkeys (*Cercopithecus*
608 *mitis*). *Behaviour*, 139(2), 291–314.
- 609 Croft, D. P., Hamilton, P. B., Darden, S. K., Jacoby, D. M. P., James, R.,
610 Bettaney, E. M., & Tyler, C. R. (2012). The role of relatedness in structuring
611 the social network of a wild guppy population. *Oecologia*, 170(4), 955–963.
612 <https://doi.org/10.1007/s00442-012-2379-8>
- 613 Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause,
614 J. (2005). Assortative interactions and social networks in fish. *Oecologia*,
615 143(2), 211–219. <https://doi.org/10.1007/s00442-004-1796-8>
- 616 Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R.
617 (2009). Behavioural trait assortment in a social network: Patterns and
618 implications. *Behavioral Ecology and Sociobiology*, 63(10), 1495–1503.
619 <https://doi.org/10.1007/s00265-009-0802-x>
- 620 Daura-Jorge, F. G., Cantor, M., Ingram, S. N., Lusseau, D., & Simões-Lopes, P.
621 C. (2012). The structure of a bottlenose dolphin society is coupled to a
622 unique foraging cooperation with artisanal fishermen. *Biology Letters*, 8(5),
623 702–705. <https://doi.org/10.1098/rsbl.2012.0174>
- 624 de Ruiter, J. R., & Geffen, E. (1998). Relatedness of matriline, dispersing males
625 and social groups in long-tailed macaques (*Macaca fascicularis*).

- 626 *Proceedings of the Royal Society B: Biological Sciences*, 265, 79–87.
627 <https://doi.org/10.1017/CBO9781107415324.004>
- 628 Dekker, D., Krackhardt, D., & Snijders, T. A. B. (2007). Sensitivity of MRQAP
629 tests to collinearity and autocorrelation conditions. *Psychometrika*, 72(4),
630 563–581. <https://doi.org/10.1007/s11336-007-9016-1>
- 631 Doreian, P., & Conti, N. (2012). Social context, spatial structure and social
632 network structure. *Social Networks*, 34(1), 32–46.
633 <https://doi.org/10.1016/j.socnet.2010.09.002>
- 634 Eberle, M., & Kappeler, P. M. (2006). Family insurance: Kin selection and
635 cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioral*
636 *Ecology and Sociobiology*, 60(4), 582–588. [https://doi.org/10.1007/s00265-](https://doi.org/10.1007/s00265-006-0203-3)
637 [006-0203-3](https://doi.org/10.1007/s00265-006-0203-3)
- 638 Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: the
639 importance of the utilization distribution. *The Journal of Wildlife*
640 *Management*, 69(4), 1346–1359.
- 641 Firth, J. A., Voelkl, B., Crates, R. A., Aplin, L. M., Biro, D., Croft, D. P., &
642 Sheldon, B. C. (2017). Wild birds respond to flockmate loss by increasing
643 their social network associations to others. *Proceedings of the Royal Society*
644 *B: Biological Sciences*, 284(1854). <https://doi.org/10.1098/rspb.2017.0299>
- 645 Fletcher, J. A., & Doebeli, M. (2009). A simple and general explanation for the
646 evolution of altruism. *Proceedings of the Royal Society B: Biological*
647 *Sciences*, 276(1654), 13–19. <https://doi.org/10.1098/rspb.2008.0829>
- 648 Frère, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson,
649 E. M., ... Sherwin, W. B. (2010). Home range overlap, matrilineal and
650 biparental kinship drive female associations in bottlenose dolphins. *Animal*
651 *Behaviour*, 80(3), 481–486. <https://doi.org/10.1016/j.anbehav.2010.06.007>
- 652 Gero, S., Gordon, J., & Whitehead, H. (2015). Individualized social preferences
653 and long-term social fidelity between social units of sperm whales. *Animal*
654 *Behaviour*, 102, 15–23. <https://doi.org/10.1016/j.anbehav.2015.01.008>
- 655 Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H.,
656 Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary
657 aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*,
658 67(3), 373–381. <https://doi.org/10.1007/s00265-012-1457-6>
- 659 Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild
660 chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in
661 cooperation. *Behavioral Ecology and Sociobiology*, 62(11), 1831–1842.
662 <https://doi.org/10.1007/s00265-008-0612-6>
- 663 Ginsberg, J. R., & Young, T. P. (1992). Measuring association between
664 individuals or groups in behavioural studies. *Animal Behaviour*, 44(PART 2),
665 377–379. [https://doi.org/10.1016/0003-3472\(92\)90042-8](https://doi.org/10.1016/0003-3472(92)90042-8)
- 666 Glander, K. E. (1993). Capture and marking techniques for arboreal primates. In
667 A. Estrada, E. Rodriguez-Luna, R. Lopez-Wilchis, & R. Coates-Estrada
668 (Eds.), *Estudios Primatológicos en Mexico, Vol. 1* (pp. 299–304).
- 669 Godde, S., Côté, S. D., & Réale, D. (2015). Female mountain goats, *Oreamnos*
670 *americanus*, associate according to kinship and reproductive status. *Animal*
671 *Behaviour*, 108, 101–107. <https://doi.org/10.1016/j.anbehav.2015.07.005>

- 672 Griffiths, S. W., & Armstrong, J. D. (2002). Kin-biased territory overlap and food
673 sharing among Atlantic salmon juveniles. *Journal of Animal Ecology*, 71(3),
674 480–486. <https://doi.org/10.1046/j.1365-2656.2002.00614.x>
- 675 Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of*
676 *Theoretical Biology*, 7(1), 1–16. [https://doi.org/10.1016/0022-](https://doi.org/10.1016/0022-5193(64)90038-4)
677 5193(64)90038-4
- 678 Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, 11(1),
679 1–17.
- 680 Hirsch, B. T., Prange, S., Hauver, S. A., & Gehrt, S. D. (2013). Genetic
681 relatedness does not predict racoon social network structure. *Animal*
682 *Behaviour*, 85(2), 463–470. <https://doi.org/10.1016/j.anbehav.2012.12.011>
- 683 Kohn, G. M., Meredith, G. R., Magdaleno, F. R., King, A. P., & West, M. J.
684 (2015). Sex differences in familiarity preferences within fission-fusion brown-
685 headed cowbird, *Molothrus ater*, flocks. *Animal Behaviour*, 106, 137–143.
686 <https://doi.org/10.1016/j.anbehav.2015.05.023>
- 687 Kossinets, G., & Watts, D. J. (2006). Empirical analysis of an evolving social
688 network. *Science*, 311, 88–90. <https://doi.org/10.1126/science.1116869>
- 689 Langergraber, K. E. (2012). Kinship and cooperation in primates. In *The*
690 *Evolution of Primate Societies* (pp. 491–513).
- 691 Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of
692 kinship on cooperation in wild chimpanzees. *Proceedings of the National*
693 *Academy of Sciences*, 104(19), 7786–7790.
694 <https://doi.org/10.1073/pnas.0611449104>
- 695 Langergraber, K. E., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in
696 female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*,
697 71(10), 840–851. <https://doi.org/10.1002/ajp.20711>
- 698 Leu, S. T., Bashford, J., Kappeler, P. M., & Bull, C. M. (2010). Association
699 networks reveal social organization in the sleepy lizard. *Animal Behaviour*,
700 79(1), 217–225. <https://doi.org/10.1016/j.anbehav.2009.11.002>
- 701 Longmire, J. L., Gee, G. F., Hardekopf, C. L., Graham, A., & Mark, G. A. (1992).
702 Establishing paternity in whooping cranes (*Grus americana*) by DNA
703 analysis. *The Auk*, 109(3), 522–529.
- 704 Louis, E. E., Ratsimbazafy, J. H., Razakamaharao, V. R., Pierson, D. J., Barber,
705 R. C., & Brenneman, R. A. (2005). Conservation genetics of black and white
706 ruffed lemurs, *Varecia variegata*, from Southeastern Madagascar. *Animal*
707 *Conservation*, 8(1), 105–111. <https://doi.org/10.1017/S1367943004001891>
- 708 Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in
709 their social networks. *Proceedings of the Royal Society B: Biological*
710 *Sciences*, 271(SUPPL. 6), 477–481. <https://doi.org/10.1098/rsbl.2004.0225>
- 711 Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K.
712 M., ... Thompson, P. M. (2006). Quantifying the influence of sociality on
713 population structure in bottlenose dolphins. *Journal of Animal Ecology*,
714 75(1), 14–24. <https://doi.org/10.1111/j.1365-2656.2005.01013.x>
- 715 Maher, C. R. (2009). Genetic relatedness and space use in a behaviorally flexible
716 species of marmot, the woodchuck (*Marmota monax*). *Behavioral Ecology*
717 *and Sociobiology*, 63(6), 857–868. <https://doi.org/10.1007/s00265-009-0726->

- 718 5
719 Mantel, N. (1967). The Detection of Disease Clustering and a Generalized
720 Regression Approach. *Cancer Research*, 27(2 Part 1), 209 LP – 220.
721 Retrieved from
722 http://cancerres.aacrjournals.org/content/27/2_Part_1/209.abstract
723 McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs
724 as repositories of social knowledge in African elephants. *Science*, 292, 491–
725 494. <https://doi.org/10.1126/science.1057895>
726 McDonald, D. B. (2007). Predicting fate from early connectivity in a social
727 network. *Proceedings of the National Academy of Sciences of the United*
728 *States of America*, 104(26), 10910–10914.
729 <https://doi.org/10.1073/pnas.0701159104>
730 Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation
731 and kinship in wild chimpanzees. *Animal Behaviour*, 59(4), 885–893.
732 <https://doi.org/10.1006/anbe.1999.1389>
733 Moscovice, L. R., Douglas, P. H., Martinez-Iñigo, L., Surbeck, M., Vigilant, L., &
734 Hohmann, G. (2017). Stable and fluctuating social preferences and
735 implications for cooperation among female bonobos at LuiKotale, Salonga
736 National Park, DRC. *American Journal of Physical Anthropology*, 163(1),
737 158–172. <https://doi.org/10.1002/ajpa.23197>
738 Mourier, J., Vercelloni, J., & Planes, S. (2012). Evidence of social communities in
739 a spatially structured network of a free-ranging shark species. *Animal*
740 *Behaviour*, 83(2), 389–401. <https://doi.org/10.1016/j.anbehav.2011.11.008>
741 Nystrand, M. (2007). Associating with kin affects the trade-off between energy
742 intake and exposure to predators in a social bird species. *Animal Behaviour*,
743 74(3), 497–506. <https://doi.org/10.1016/j.anbehav.2006.11.031>
744 Peakall, R., & Smouse, P. E. (2012). GenALEX 6.5: Genetic analysis in Excel.
745 Population genetic software for teaching and research-an update.
746 *Bioinformatics*, 28(19), 2537–2539.
747 <https://doi.org/10.1093/bioinformatics/bts460>
748 Perry, S. (2012). *The Behavior of Wild White-Faced Capuchins. Advances in the*
749 *Study of Behavior* (1st ed., Vol. 44). Elsevier Inc.
750 <https://doi.org/10.1016/b978-0-12-394288-3.00004-6>
751 Podgórski, T., Lusseau, D., Scandura, M., Sönrichsen, L., & Jędrzejewska, B.
752 (2014). Long-lasting, kin-directed female interactions in a spatially structured
753 wild boar social network. *PLoS ONE*, 9(6), 1–11.
754 <https://doi.org/10.1371/journal.pone.0099875>
755 Pope, T. R. (2000). Reproductive success increases with degree of kinship in
756 cooperative coalitions of female red howler monkeys (*Alouatta seniculus*).
757 *Behavioral Ecology and Sociobiology*, 48(4), 253–267.
758 <https://doi.org/10.1007/s002650000236>
759 Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic
760 markers. *Evolution*, 43(2), 258–275.
761 Radespiel, U., Lutermann, H., Schmelting, B., Bruford, M. W., & Zimmermann, E.
762 (2003). Patterns and dynamics of sex-biased dispersal in a nocturnal
763 primate, the grey mouse lemur, *Microcebus murinus*. *Animal Behaviour*,

- 764 65(4), 709–719. <https://doi.org/10.1006/anbe.2003.2121>
- 765 Ramos-Fernández, G., Boyer, D., Aureli, F., & Vick, L. G. (2009). Association
766 networks in spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and*
767 *Sociobiology*, 63(7), 999–1013. <https://doi.org/10.1007/s00265-009-0719-4>
- 768 Riehl, C. (2011). Living with strangers: direct benefits favour non-kin cooperation
769 in a communally nesting bird. *Proceedings of the Royal Society B: Biological*
770 *Sciences*, 278(1712), 1728–1735. <https://doi.org/10.1098/rspb.2010.1752>
- 771 Salpeteur, M., Patel, H., Balbo, A. L., Rubio-Campillo, X., Madella, M.,
772 Ajithprasad, P., & Reyes-García, V. (2015). When knowledge follows blood:
773 Kin groups and the distribution of traditional ecological knowledge in a
774 community of seminomadic pastoralists, Gujarat (India). *Current*
775 *Anthropology*, 56(3), 471–483. <https://doi.org/10.1086/681006>
- 776 Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds
777 enhance reproductive success in male macaques. *Current Biology*, 20(24),
778 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- 779 Seyfarth, R. M., & Cheney, D. L. (2012). The Evolutionary Origins of Friendship.
780 *Annual Review of Psychology*, 63(1), 153–177.
781 <https://doi.org/10.1146/annurev-psych-120710-100337>
- 782 Silk, J. B. (2002). Kin selection in primate groups. *International Journal of*
783 *Primatology*, 23(4), 849–875. <https://doi.org/10.1023/A:1015581016205>
- 784 Silk, J. B. (2007). The adaptive value of sociality in mammalian groups.
785 *Philosophical Transactions of the Royal Society B: Biological Sciences*,
786 362(1480), 539–559. <https://doi.org/10.1098/rstb.2006.1994>
- 787 Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social Bonds of Female Baboons
788 Enhance Infant Survival. *Science*, 302, 1231–1234.
789 <https://doi.org/10.1126/science.1088580>
- 790 Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult
791 female baboons (*Papio cynocephalus*) II. Variation in the quality and stability
792 of social bonds. *Behavioral Ecology and Sociobiology*, 61(2), 197–204.
793 <https://doi.org/10.1007/s00265-006-0250-9>
- 794 Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult
795 female baboons (*papio cynocephalus*) I. Variation in the strength of social
796 bonds. *Behavioral Ecology and Sociobiology*, 61(2), 183–195.
797 <https://doi.org/10.1007/s00265-006-0249-2>
- 798 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice,
799 L. R., ... Cheney, D. L. (2009). The benefits of social capital: Close social
800 bonds among female baboons enhance offspring survival. *Proceedings of*
801 *the Royal Society B: Biological Sciences*, 276(1670), 3099–3104.
802 <https://doi.org/10.1098/rspb.2009.0681>
- 803 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice,
804 L. R., ... Cheney, D. L. (2010a). Female chacma baboons form strong,
805 equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*,
806 64(11), 1733–1747. <https://doi.org/10.1007/s00265-010-0986-0>
- 807 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice,
808 L. R., ... Cheney, D. L. (2010b). Strong and consistent social bonds enhance
809 the longevity of female baboons. *Current Biology*, 20(15), 1359–1361.

- 810 <https://doi.org/10.1016/j.cub.2010.05.067>
- 811 Smith, J. E. (2014). Hamilton's legacy: Kinship, cooperation and social tolerance
812 in mammalian groups. *Animal Behaviour*, 92, 291–304.
813 <https://doi.org/10.1016/j.anbehav.2014.02.029>
- 814 Spiegel, O., Sih, A., Leu, S. T., & Bull, C. M. (2018). Where should we meet?
815 Mapping social network interactions of sleepy lizards shows sex-dependent
816 social network structure. *Animal Behaviour*, 136, 207–215.
817 <https://doi.org/10.1016/j.anbehav.2017.11.001>
- 818 Stanley, C. R., Mettke-Hofmann, C., Hager, R., & Shultz, S. (2018). Social
819 stability in semiferrous ponies: networks show interannual stability alongside
820 seasonal flexibility. *Animal Behaviour*, 136, 175–184.
821 <https://doi.org/10.1016/j.anbehav.2017.04.013>
- 822 Stone, J., & Björklund, M. (2001). DELRIOUS: A computer program designed to
823 analyse molecular marker data and calculate delta and relatedness
824 estimates with confidence. *Molecular Ecology Notes*, 1(3), 209–212.
825 <https://doi.org/10.1046/j.1471-8278.2001.00034.x>
- 826 Strickland, K., Gardiner, R., Schultz, A. J., & Frère, C. H. (2014). The social life of
827 eastern water dragons: Sex differences, spatial overlap and genetic
828 relatedness. *Animal Behaviour*, 97, 53–61.
829 <https://doi.org/10.1016/j.anbehav.2014.08.009>
- 830 Strickland, K., Levengood, A., Foroughirad, V., Mann, J., Krzyszczyk, E., & Frère,
831 C. H. (2017). A framework for the identification of long-term social avoidance
832 in longitudinal datasets. *Royal Society Open Science*, 4(8).
833 <https://doi.org/10.1098/rsos.170641>
- 834 Taberlet, P. (1996). Reliable genotyping of samples with very low DNA quantities
835 using PCR. *Nucleic Acids Research*, 24(16), 3189–3194.
836 <https://doi.org/10.1093/nar/24.16.3189>
- 837 Vasey, N. (2006). Impact of seasonality and reproduction on social structure,
838 ranging patterns and fission–fusion social organization in red ruffed lemurs.
839 In *Lemurs: ecology and adaptation* (pp. 275–305). New York:
840 Springer/Kluwer.
- 841 Wahaj, S. A., Van Horn, R. C., Van Horn, T. L., Dreyer, R., Hilgrs, R., Schwarz,
842 J., & Holekamp, K. E. (2004). Kin discrimination in the spotted hyena
843 (*Crocuta crocuta*): Nepotism among siblings. *Behavioral Ecology and*
844 *Sociobiology*, 56(3), 237–247. <https://doi.org/10.1007/s00265-004-0783-8>
- 845 Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis
846 of animal behaviour: a promising tool for the study of sociality. *Animal*
847 *Behaviour*, 75(2), 333–344. <https://doi.org/10.1016/j.anbehav.2007.06.020>
- 848 Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental
849 care in sperm whales. *Behavioral Ecology & Sociobiology*, 38(4), 237–244.
- 850 Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative methods for*
851 *vertebrate social analysis*. Chicago: University of Chicago Press.
- 852 Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures.
853 *Behavioral Ecology and Sociobiology*, 63(5), 765–778.
854 <https://doi.org/10.1007/s00265-008-0697-y>
- 855 Wilkinson, G. S., Carter, G. G., Bohn, K. M., & Adams, D. M. (2016). Non-kin

856 cooperation in bats. *Philosophical Transactions of the Royal Society B:*
857 *Biological Sciences*, 371(1687). <https://doi.org/10.1098/rstb.2015.0095>
858 Wiszniewski, J., Allen, S. J., & Möller, L. M. (2009). Social cohesion in a
859 hierarchically structured embayment population of Indo-Pacific bottlenose
860 dolphins. *Animal Behaviour*, 77(6), 1449–1457.
861 <https://doi.org/10.1016/j.anbehav.2009.02.025>
862 Wright, P. C., Erhart, E. M., Tecot, S., Baden, A. L., Arrigo-nelson, S. J., Herrera,
863 J., ... Zohdy, S. (2012). *Long-Term Field Studies of Primates*.
864 <https://doi.org/10.1007/978-3-642-22514-7>