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

ABSTRACT

Fission-fusion social dynamics are common among a number of vertebrate taxa, and yet the factors shaping these variable associations among subgroup members have not been widely addressed. Associations may occur simply because of shared habitat preferences; however, social ties may also be influenced by genetic relatedness (kinship) or social attraction. Here, we investigate the association patterns of wild black-and-white ruffed lemurs, *Varecia variegata*, in Ranomafana National Park, Madagascar using behavioural, spatial (home range), and genetic data from twenty-four individually identified animals. We collected 40,840 records of group composition over a 17-month period and from this calculated pairwise association indices. We also used ranging coordinates and genetic samples to estimate patterns of spatial overlap and kinship, and then related these measures to patterns of affiliation. From these analyses, we found that dyadic ruffed lemur social associations were generally sparse and weak; that home range overlap was minimal; and that average relatedness within the community was low. We found no evidence that kinship was related to patterns of either spatial overlap or social association; instead, associations were primarily driven by space use. Moreover, social preferences were unrelated to kinship. While home range overlap explained most of the variation seen in social association, some variation remains unaccounted

for, suggesting that other social, ecological, and biological factors such as shared resource defense or communal breeding might also play a role in social attraction. Our results further highlight the need to consider individual space use and nuances of species behavior when investigating social preference and social association more generally.

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

INTRODUCTION

Animal social systems reflect non-random relationships among neighbouring conspecifics, the content, quality, and patterning of which define their social structure (Hinde, 1976). In fact, there is growing evidence that taxa as diverse as fishes, lizards, birds, cetaceans, and equids exhibit social associations and interactions that are not only non-random, but highly structured (Augusto, Frasier, & Whitehead, 2017; Croft et al., 2012, 2005; Firth et al., 2017; Spiegel, Sih, Leu, & Bull, 2018; Stanley, Mettke-Hofmann, Hager, & Shultz, 2018). Individuals vary in the numbers, strengths, and stabilities of their social ties (Croft et al., 2005; McDonald, 2007; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006; Silk et al., 2010a; Stanley et al., 2018), as well as in their preferences for particular social associates (e.g., Cords, 2002; Gero, Gordon, & Whitehead, 2015; Kohn, Meredith, Magdaleno, King, & West, 2015; Mourier, Vercelloni, & Planes, 2012; Perry, 2012; Schülke, Bhagavatula, Vigilant, &

Ostner, 2010)—outcomes of which can be evolutionarily significant (Seyfarth & Cheney, 2012; Silk, 2007). For example, the extent, strength, and nature of females' social relationships have been positively linked to higher fertility (*Macaca mulatta*: Brent et al., 2013; humans: Balbo & Barban, 2014), longer lifespan (*Papio cynocephalus*: Alberts, 2019; Archie, Tung, Clark, Altmann, & Alberts, 2014; *Papio ursinus:* Silk et al., 2010b), and greater offspring survival (*Equus caballus*: Cameron, Setsaas, & Linklater, 2009; *Papio cynocephalus*: Silk, Alberts, & Altmann, 2003; *Papio ursinus:* Cheney, Silk, & Seyfarth, 2016; Silk et al., 2009; *Physeter microcephalus*: Whitehead, 1996). Similarly, males that form strong social bonds have been shown to be more successful at forming coalitions, achieving high rank, and siring more offspring than males with weaker social bonds (e.g., *Chiroxiphia linearis*: McDonald, 2007; *Macaca assamensis*: Schülke et al., 2010; *Pan troglodytes*: Gilby et al., 2013). Nevertheless, while the long-term health and fitness outcomes of sociality have been the focus of much investigation, until recently the factors shaping social preferences have received comparatively less attention.

Several hypotheses have been proposed to explain social association, the most popular being kinship, whereby group members preferentially associate with and, in the case of kin selection, are more likely to direct costly altruistic behaviours toward close genetic relatives (Hamilton, 1964). For instance, many female mammals associate with and exhibit social preferences toward maternal kin (Smith, 2014), a pattern observed in primates in particular (reviewed in Langergraber, 2012), but also in spotted hyaenas (Wahaj et al., 2004), African

elephants (Archie, Moss, & Alberts, 2006), dolphins (Frère et al., 2010), and mountain goats (Godde, Côté, & Réale, 2015), among others. Social preferences toward kin can be driven by the benefits of associating with relatives, such as allomaternal care (reviewed in Briga, Pen, & Wright, 2012; Pope, 2000; and in some cases even brood parasitism, Andersson, 2017), reduced aggression and infanticide risk (reviewed in Brown & Brown, 1996; Agrell, Wolff, & Ylonen, 1998), foraging advantages (Griffiths & Armstrong, 2002; Nystrand, 2007), and shared social and ecological knowledge (McComb, Moss, Durant, Baker, & Sayialel, 2001; Salpeteur et al., 2015). However, social associations have also been linked to direct fitness consequences among nonrelatives (Baden, Wright, Louis, & Bradley, 2013; Cameron et al., 2009; G. G. Carter & Wilkinson, 2015; McFarland et al. 2017; Riehl, 2011), suggesting that social preferences can evolve based on direct benefits alone. Moreover, evidence for kin-biased relationships in other species, particularly those with higher fission-fusion dynamics, is weak (e.g., Best, Dwyer, Seddon, & Goldizen, 2014; K. D. Carter, Seddon, Frère, Carter, & Goldizen, 2013; Hirsch, Prange, Hauver, & Gehrt, 2013; Langergraber, Mitani, & Vigilant, 2007, 2009; Moscovice et al., 2017; Wilkinson, Carter, Bohn, & Adams, 2016), raising questions as to the ubiquity of kinship in the formation and maintenance of social bonds.

One complicating factor in determining whether and how kinship shapes social preference is that it can be difficult to decouple social associations due to kinship from associations due to other social and spatial contexts (reviewed in Doreian & Conti, 2012; Wey, Blumstein, Shen, & Jordán, 2008). For example, in

some species it is difficult to differentiate whether strong associations are due to strong genetic ties or to other factors, such as sex or age (Lusseau & Newman, 2004; Mourier et al., 2012), habitat utilization (Wiszniewski, Allen, & Möller, 2009), or foraging specializations (Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012; Gilby & Wrangham, 2008; Griffiths & Armstrong, 2002; Mitani, Merriwether, & Zhang, 2000). Indeed, patterns of social association have been found to correlate with spatial overlap (i.e., overlapping home ranges) more strongly than, or to the exclusion of, kinship in a number of species (Best et al., 2014; K. D. Carter et al., 2013; Frère et al., 2010; Strickland, Gardiner, Schultz, & Frère, 2014). Moreover, although individuals living in closer physical proximity are more prone to interact (e.g., Clutton-Brock, 1989; Kossinets & Watts, 2006), conspecifics with high levels of spatial overlap may also mediate their interactions by temporally modifying range use, such that animals with highly overlapping ranges may interact minimally, if at all (e.g., temporal avoidance) (Leu, Bashford, Kappeler, & Bull, 2010; Ramos-Fernández, Boyer, Aureli, & Vick, 2009; Strickland et al., 2017). While still uncommon, studies that consider the simultaneous effects of spatial overlap and kinship on association patterns are thus important to understanding the role of social preference in the evolution of social systems and sociality (e.g., Best et al., 2014; K. D. Carter et al., 2013; Frère et al., 2010; Lusseau et al., 2006; Maher, 2009; Podgórski, Lusseau, Scandura, Sönnichsen, & Jędrzejewska, 2014; Strickland et al., 2014; Piza-Roca et al. 2019).

Ruffed lemurs (Genus *Varecia*) are moderately-sized frugivores (Baden,

116 Brenneman, & Louis Jr., 2008; Balko & Underwood, 2005) that live in groups
117 (hereafter "communities") comprising as many as 30 adult and subadult
118 individuals and their offspring (Baden, Webster, & Kamilar, 2016 and references
119 therein). From earlier work, we know that communities are characterized by high
120 fission-fusion dynamics (*sensu* Kummer 1971), with members associating in fluid
121 subgroups (or '"parties") that vary in size, cohesion, membership, and duration
122 (Baden, Webster, & Kamilar, 2016). Within communities, there is striking
123 variation in individual ranging behavior, degree of home range overlap with other
124 community members, and the number and strength of social associations
125 (Baden, 2011; Baden & Gerber, n.d.; Baden et al., 2016; Vasey, 2006).
126 Individuals never use the entire communal territory, instead concentrating their
127 ranging to proportionately smaller areas that overlap with as few as four (25%) to
128 as many as twelve (75%) other community members (Baden & Gerber, n.d.).
129 Association patterns are equally variable, with individuals associating in
130 subgroups with anywhere from one to ten individuals throughout the year (Baden
131 et al. 2016). Overall, associations are generally weak, and animals spend nearly
132 half of their time alone (Baden et al. 2016). Nevertheless, certain individuals
133 appear to preferentially associate and are regularly found together in "core
134 groups" whose members are characterized by both high association strength and
135 home range overlap (Vasey 2006; Morland 1991a,b; Baden 2011). Moreover,
136 studies of microsatellite STR markers and mitochondrial DNA have shown that,
137 while average pairwise relatedness within communities is low (i.e., both sexes
138 disperse: Baden et al., 2014), communities nevertheless contain relatives (e.g,

Baden, 2011; Baden et al., 2013). Taken together, these lines of evidence suggest that during subgroup formation community members may be actively choosing social associates, and that these associations may be shaped by a number of ecological, social, and biological factors. Here, we hypothesize (H1) that social associations among members of a black-and-white ruffed lemur (*Varecia variegata*) community are driven by space use and kinship. Specifically, we quantify dyadic measures of association strength, spatial overlap, and relatedness to test the predictions that members with higher home range overlap (P1.1) and relatedness (P1.2) will associate more often than dyads which exhibit disparate range use or are unrelated. Moreover, because previous studies have found a relationship between social preference and kinship, we further hypothesize (H2) that relatedness will drive association preferences (P2.1), with preferred associates being more related than non-preferred dyads.

METHODS

Study site and subjects

We collected data from one *V. variegata* community at Mangevo [21°220 6000 S, 47°280 000 E], a mid-elevation (660-1,200 m) primary rainforest site located in the southeastern parcel of Ranomafana National Park, Madagascar (Wright et al., 2012) during 16 months of study (August–December 2007; February– December 2008). At the time of the study, the community included 24 adults and subadults (8 adult females, 11 adult males, 5 subadult males). All individuals in this study were habituated and individually identified via radio-

collars or unique collar-tag combinations prior to behavioural observations (see Baden et al., 2016 for specific details; see also Ethical note below). Animals were collared under veterinary supervision following a strict protocol (Glander, 1993). Nineteen infants were born in the 2008 birth season and were present from October to December 2008, when the study ended. Sampling efforts resulted in a total of 4,044 focal observation hours.

Ethical note

All animal protocols adhere to the guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2019). Subjects were habituated to researcher presence as part of a long-term study established in 2005. Since 2005, subjects have been periodically immobilized in the field (approximately once every 2 to 3 years) for application or replacement of radio-transmitter collars, which allow researchers to accurately identify individuals and locate and track them in the field during behavioral observations. Immobilization and sampling procedures adhered to the protocols established by Glander (1993) and have been implemented by Dr. Randall Junge (MS, DVM, Dipl American College of Zoological Medicine, Dipl American College of Animal Welfare), Director of the Prosimian Biomedical Survey Project (PBSP), since 2000. During captures, each lemur is immobilized by remote injection with tiletamine/zolazepam. Animals are examined immediately upon capture, and once determined to be stable they are transported back to the basecamp for examination (not more than 15 minutes). Animals are evaluated again for

185 stability, and monitored by a licensed veterinarian (Dr. Junge) throughout the
186 anesthesia. Biological samples, including blood (no more than 1 ml per kilogram)
187 for genetic analysis and biomedical health assessments, are collected for later
188 analysis. Lemurs are given a balanced electrolyte solution (30 ml)
189 subcutaneously and are monitored until recovery. Once fully recovered, lemurs
190 are released at the site of capture. Anesthetic episodes typically last 1 hour or
191 less. Lemurs that are adequately awake by midafternoon (3 PM) are released the
192 same day. Those that are not adequately recovered are held overnight in cloth
193 bags and released before 10 AM the next morning. As ruffed lemurs are diurnal,
194 releasing animals with residual sedation in the late afternoon could predispose
195 them to predation. This capture, monitoring, sampling and release protocol has
196 been used successfully by PBSP veterinarians for 15 years, on 44 trips to 18
197 sites throughout Madagascar. Biomedical health assessments by Dr. Junge and
198 population genetic assessments by Baden et al. (2014, 2019) are integral parts
199 of population management, as they are used to identify heath concerns such as
200 introduction of human or livestock parasites to the site (as documented in other
201 parts of Ranomafana National Park) and inbreeding depression. They are also
202 useful for identifying health parameters in a population inhabiting a pristine forest,
203 allowing that information to be used as a benchmark to evaluate this and other
204 populations should they experience epidemic disease or population decline.
205 Observers never interact with subjects outside of the capture period. Utmost care
206 was taken to minimize the impact of our presence on our subjects during
207 captures and subsequent behavioral observations. Observations were conducted

208 noninvasively at a minimum observer distance of 10 m from the focal subject.
209 When in the presence of subjects, observers speak quietly and make efforts to
210 not disturb the individual. No more than four observers are allowed to participate
211 in observations at any one time. Subjects were target for focal observations, at
212 most, twice per month. Permission to conduct research was granted by
213 Madagascar's National Parks (ANGAP/MNP, #084/07-041/08). Research
214 protocols were approved by and in compliance with Stony Brook University
215 IACUC #2005-20081449.
216

217 **Data collection**

218 *Behavioural monitoring*

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

228 Upon initial contact with the focal individual, we recorded the number and
229 identities of all other individuals present within the subgroup. To do so, one
230 observer remained with the focal individual while the remaining three team

231 members spread out to locate and identify all other members of the subgroup. *A*
232 *priori*, individuals were considered members of a subgroup only if they were
233 within 50 m of the group center and were seen associating, traveling with and
234 maintaining proximity to members of the subgroup being followed. However, an
235 earlier study found that average group spread in this population ranged between
236 6 to 15 m, and rarely exceeded 30 m (Baden et al. 2016). Thus, while subgroup
237 membership was operationalized to include all members within 50 m, effective
238 subgroup spread was typically much smaller (see Baden et al., 2016 for details).
239 After initial contact, we monitored subsequent changes in subgroup size,
240 composition (age/sex class, individual identity), and cohesion (i.e., the greatest
241 distance between any two subgroup members), as well as activity state of the
242 focal subject using instantaneous scan sampling techniques collected at 5 min
243 intervals (Altmann, 1974). Sampling efforts resulted in a total of 4,044 focal
244 observation hours, during which time we recorded 40,840 group scans.
245 We collected simultaneous GPS coordinates at 10 min intervals from as
246 close to the focal individual as possible to document daily individual range use.
247 We recorded spatial coordinates only if estimated positional error was less than
248 10 m.
249
250 *Genetic sampling*
251 In addition, we collected genetic samples from 38 black-and-white ruffed
252 lemurs from the Mangevo population, including all subjects in this study, during
253 five capture seasons spanning four consecutive years (2005-2008; see Baden,

254 2011 for details). Sample collection occurred under veterinary supervision and
255 followed a strict protocol outlined by Glander (1993). All capture procedures
256 occurred during non-reproductive seasons in the absence of infants and
257 dependent offspring.

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

267

268 **Data analysis**

269 *Social association*

270 In this study, we define social association as individuals being present in
271 the same subgroup at the same time. We considered social preferences to occur
272 (that is, the dyad was composed of "preferred associates") when dyads had a
273 significantly stronger strength of association than other dyads in the community
274 (see "Relatedness among preferred associates" below). This species is typically
275 described as being "female-bonded" (Morland 1991a), in line with the definition
276 that to be 'socially bonded' requires that multiple, independent types of

277 associations or interactions are significantly higher than expected (Whitehead,
278 2008). We do not examine social bonds in this study because we only focus on a
279 single measure of association. Finally, we also use the term “social tie” in the
280 network sense (e.g., Wasserman and Faust, 1994; Croft et al., 2008): individuals
281 that have a social tie have a nonzero association index and a “stronger tie” has a
282 higher association index.

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

292 We used SOCPROG 2.9 (Whitehead, 2009) to calculate association
293 indices (AIs) between all pairs (i.e., dyads) of individuals using the “simple ratio”
294 index, which quantifies the proportion of time that two individuals are observed
295 together relative to their total observation time overall. This index is appropriate
296 when individuals are equally likely to be correctly identified (Cairns & Schwager,
297 1987; Ginsberg & Young, 1992; Whitehead, 2008), which is the case for this
298 population. Given that subgroup composition in this community changes
299 approximately every 90 minutes (Baden et al., 2016), we used a 6-hour sampling

interval to reduce autocorrelation among periods. We also removed any subject observed in fewer than 10 sampling periods. Our final dataset (overall dataset) included 8 adult females and 9 adult males totaling 136 dyads observed in over 11,171 point scans.

To examine seasonal variation in associations, we organized the subsetted data from 2008 into three seasons according to female reproductive state as defined by Baden et al. (2013). Using the protocols described above, our final datasets included: 8 females and 9 males over 5,051 scans during the nonbreeding season (January through June); 7 females and 8 males over 3,267 scans during the mating/gestation season (July through September); and 8 females and 6 males over 2,664 scans during the birth/lactation season (October through December). We compared distributions of AIs across seasons using a Kruskal-Wallis test implemented in R (Kruskall and Wallis, 1952).

Spatial overlap

Estimates of home range overlap used in this study come from Baden & Gerber (n.d.). Briefly, we calculated home range overlap between all pairs of individuals using a utilization distribution overlap index (UDOI; Fieberg & Kochanny, 2005) implemented in the R package adehabitat (Calenge, 2011). The UDOI is an index of space-use sharing between two utilization distributions (UDs). UDOI values can range from 0 to 1, with a UDOI of 0 indicating no home range overlap and a UDOI of 1 indicating that home ranges are uniformly distributed and have 100% overlap. Values can also be >1 if both UDs are

323 nonuniformly distributed and also have a high degree of overlap. Values <1
324 indicate less overlap relative to uniform space, whereas values >1 indicate higher
325 than normal overlap relative to uniform space. We calculated four UDOIs for all
326 pairs of individuals: one annual UDOI, and three seasonal UDOIs according to
327 female reproductive state, as for association analyses described above.
328
329 *Relatedness*
330 We genotyped individuals at a suite of 15 polymorphic microsatellite loci
331 (see Baden, 2011 and Baden et al., 2014 for details). We extracted total genomic
332 DNA from blood and/or tissue samples using standard nucleic acid extraction kits
333 (QIAamp DNA Mini Kit; Qiagen) automated on a QiaCube (Qiagen). Extraction
334 procedures followed the manufacturer's protocols, with the following modification
335 to the tissue extraction procedures: samples were allowed to lyse initially in ASL
336 buffer for 24-48 hours rather than 10 minutes.
337 We carried out PCR amplifications in a total reaction volume of 25 µl
338 consisting of 2 µl template, 12.5 µl Qiagen HotStar Taq Master Mix, and 10 µM of
339 each primer. Amplification conditions were as follows: initial denaturation at 95 °C
340 for 15 min; 35 cycles of 30 s at 94 °C, 40 s at 54 to 60 °C (see Louis et al., 2005),
341 1 min at 72 °C, and a final extension of 7 min at 72 °C. The 5′ end of the forward
342 primer was fluorescently labeled, and amplification products were separated and
343 visualized using capillary electrophoresis (ABI 3730xl Genetic Analyzer). We
344 assessed allele sizes relative to an internal size standard (ROX-500) using Gene
345 Mapper software (Applied Biosystems), and scored final genotypes based on

346 multiple independent reactions (Taberlet, 1996). Panels yielded PI_{sib} (Queller &
347 Goodnight, 1989) values of 2.7×10^{-5}, demonstrating the very low probability that
348 two individuals would share the same multilocus genotype by chance. We further
349 tested the robusticity of this suite of loci for estimating relatedness with a
350 rarefaction analysis as in Altmann & Alberts (1996) and de Ruiter & Geffen
351 (1998) using the program RE-RAT (http://people.musc.edu/~schwaclh/). We
352 estimated pairwise relatedness among individuals (*r*) following Queller & Goodnight
353 (1989) using the program GenAlEx 6.5 (Peakall & Smouse, 2012). Relatedness was
354 based on allele frequencies derived from a larger population of 38 adult multilocus
355 genotypes (Baden, 2011). Fine scale dyadic relatedness assessments (e.g.,
356 distinguishing between full and half-sibs) are not possible in most microsatellite
357 studies, and in fact, the ability to differentiate relatedness disjunctions on such a
358 scale would probably require 30 to 60 microsatellite loci (Stone & Björklund,
359 2001). We therefore consider "related dyads" to be those with r-values ≥ 0.25; we
360 made no attempt to further distinguish categories or degrees of relatedness.
361
362 *Relationships among social associations, spatial overlap, and relatedness*
363 We used a series of Mantel tests followed by a multiple regression
364 quadratic assignment procedure (MRQAP) to test our first hypothesis (H1), that
365 association strength was driven by spatial overlap and relatedness. We first used
366 Mantel tests to examine whether association indices were independently related
367 to either spatial overlap (P1.1) or relatedness (P1.2), as well as to test for a
368 correlation between spatial overlap and relatedness (Mantel, 1967). We further

369 used a multiple regression quadratic assignment procedure (MRQAP; Dekker,
370 Krackhardt, & Snijders, 2007) to determine relationships between the response
371 variable—association index—and predictor variables—sex, spatial overlap
372 (P1.1), and relatedness (P1.2). For sex, we used a matrix of sex similarity, which
373 used values of 1 (same sex) and 0 (different sex). MRQAP tests each pairwise
374 combination of response and predictor matrices while holding the remaining
375 predictor matrices constant. We performed both Mantel tests and MRQAP for the
376 overall dataset as well as in each of the three seasons using SOCPROG 2.9
377 (Whitehead, 2009).
378
379 *Relatedness among preferred associates*
380 Studies of other taxa have found that relatedness can shape social
381 preferences, even if it does not structure association among all dyads (Carter et
382 al., 2013; Best et al., 2014). Therefore, in addition to the analyses described
383 above, we used generalized linear models to test our second hypothesis (H2)
384 that relatedness between two individuals in a dyad predicted whether they were
385 "preferred" associates. Here, we define "preferred associates" (we also use
386 "social preference") as dyads exhibiting significantly higher association indices
387 than other dyads in the community.
388 We identified preferred associates in our overall dataset (described in
389 "Social association" above) using SOCPROG 2.9's (Whitehead, 2009)
390 permutation tests based on Bejder et al. (1998) with modifications by Whitehead
391 (2008). We used the "permute associations within samples" option, along with

392 1000 flips per permutation and 10,000 permutations. We classified dyads as
393 preferred associates if the dyad's AI was significantly high (one-tailed α = 0.05).
394 We next used logistic regression analysis, implemented using Scikit-learn
395 in Python (Pedregosa et al., 2011) to test if relatedness of a dyad (independent
396 variable; measured using continuous relatedness values calculated as described
397 in "Relatedness" above) predicted whether members in that dyad were preferred
398 associates (P2.1; dependent variable; binary response of "preferred" or "not"
399 based on SOCPROG permutation analyses). To assess significance, we
400 compared the coefficient of the regression model to a "null" distribution of
401 coefficients generated from 10,000 randomizations of the model. During each
402 replicate, we shuffled relatedness values among dyads before building the
403 randomized regression model. Our p-value was calculated as: 1 – (*percentile of*
404 *observed coefficient in null distribution*). The script in which we implemented this
405 procedure is available at https://github.com/thw17/Varecia_social_preferences.
406

407 **RESULTS**

408 *Social association*

409 The average overall association index (AI) was 0.05 ± 0.03 (Baden et al.,
410 2016). While we observed similar mean AIs in each of the three reproductive
411 seasons (nonbreeding = 0.04 ± 0.02; mating/gestation = 0.06 ± 0.03;
412 birth/lactation = 0.07 ± 0.03), the distributions of AIs significantly differed across
413 seasons (Kruskall-Wallis chi-squared = 8.423, df = 2, p = 0.015). Within seasons,
414 individuals also varied substantially in their AIs. Distributions were right skewed,

with many values at or near 0 and maximum values as high as 0.82. Average individual AIs (i.e., the average of all of an individual's AIs) varied from 0.01 to 0.11 (nonbreeding = 0.01-0.08; mating/gestation = 0.01-0.11; birth/lactation = 0.01-0.10), while maximum individual AIs ranged from 0.07 to 0.82 (nonbreeding = 0.08-0.82; mating/gestation = 0.07-0.79; birth/lactation = 0.08-0.82).

Spatial overlap

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

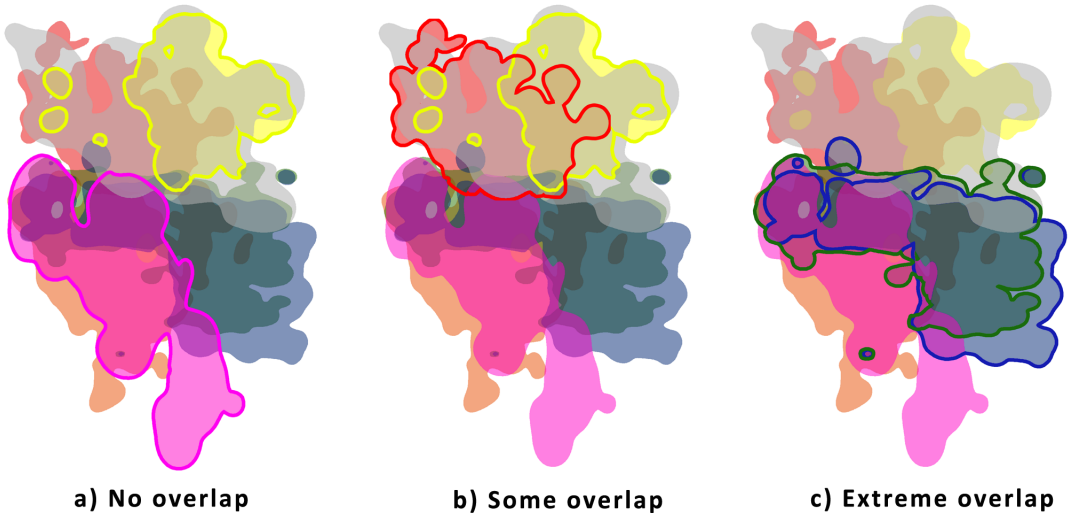

Figure 1. Examples of home range overlap among pairs of individuals within the Mangevo ruffed lemur community: a) Females Pink-Yellow and Radio-Yellow have no spatial overlap among home ranges (i.e., UDOI = 0.00), whereas b)

females Radio-Yellow and Radio-Red and c) females Radio-Blue and Radio-Green share some (UDOI = 0.106) to nearly complete home range overlap (UDOI = 0.951), respectively.

Relatedness

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

Results of the rarefaction curve (y = 0.7991, r^2 =0.9992) showed average relatedness values stabilizing after 5 loci, with the difference between mean relatedness using 5 and 6 loci changing by only 0.95% (0.023), and the difference between using 6 and 7 loci changing by only 0.56% (0.016). Thus, subsequent dyadic r-value calculations included all possible dyads (n = 703 dyads), as all individuals could be compared at 5 or more loci. Average pairwise relatedness among adults within the community was -0.06 ± 0.02 and ranged from -0.72 to 0.65 (Table 1; Figure 2).

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

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

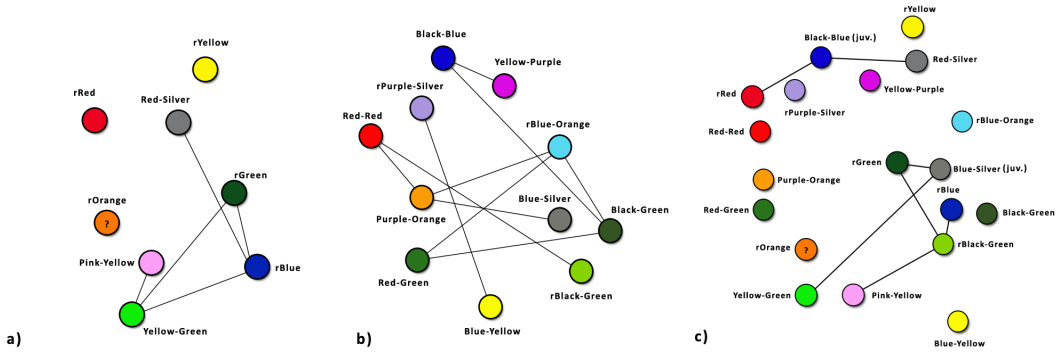

Figure 2. Pairwise genetic relatedness (r ≥ 0.25) among adult a) female-female dyads, b) male-male dyads, and c) female-male dyads within the Mangevo social community. "?" indicates individuals for which genotype data are unavailable. Nodes are organized according to individual home range centroids.

Fewer than ten percent (8.8%) of dyads within the community were genetic relatives. Despite this, more than three-quarters of adult females (n=6 of 7 for which genetic data were available; 85.7%) and all of adult males (n=11 of 11; 100%) were related (r ≥ 0.25) to at least one, and up to as many as three other same-sex relative(s) within the community (Figure 2).

Relationships among social associations, spatial overlap, and relatedness

Using the full dataset, Mantel tests revealed that kinship was unrelated to either home range overlap (UDOI; $n = 25$, $r = 0.047$ $p = 0.724$) or association indices (AI; $n = 14$, $r = 0.120$, $p = 0.294$), whereas UDOI and AI were significantly correlated ($n = 17$, $r = 0.789$, $p << 0.001$; Figure 3). This pattern held across all three reproductive seasons (Table 2). It is worth noting, however, that the correlation coefficient between UDOI and AI in the nonbreeding season was much lower, albeit still significantly positive, than the mating/gestation and birth/lactation seasons, which were very similar (Table 2). Similarly, when we used MRQAPs to jointly analyze the effects of UDOI, kinship, and sex on AI, in every time period we analyzed, the partial correlations between UDOI and AI were always significantly positive, while kinship and sex were never significantly correlated with AI (Table 3). These results support prediction P1.1, but do not support prediction P1.2.

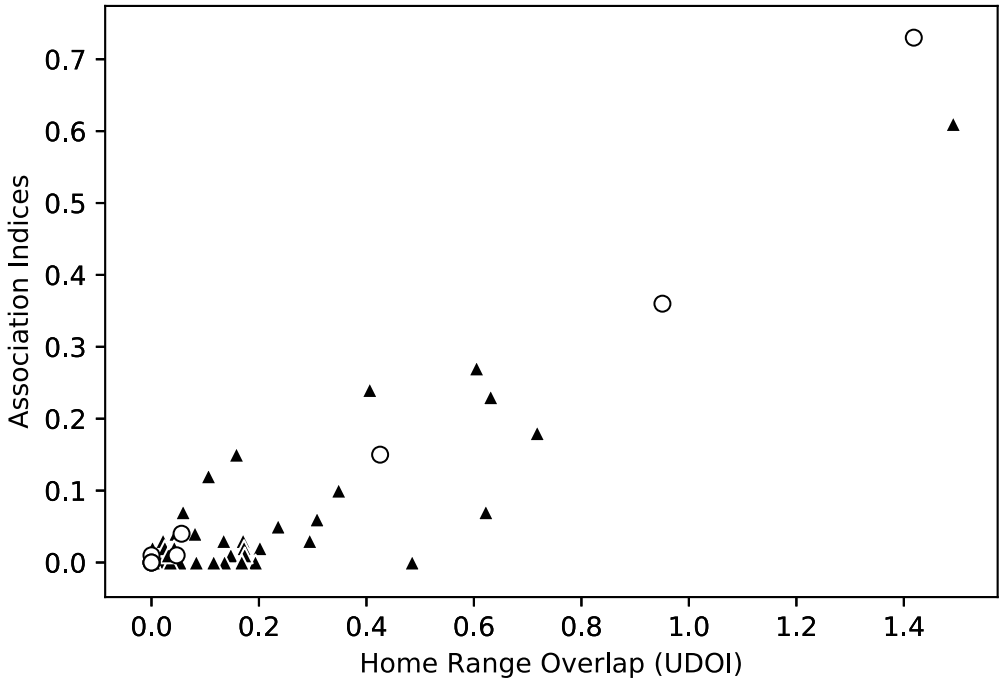

Figure 3. Scatterplot illustrating the relationship between social association (AI) and home range overlap (UDOI). AIs range from 0 (no association) to 1 (100% association). Similarly, UDOIs range from 0 (no overlap) to 1 (complete overlap); values of >1 are possible if both UDs are nonuniformly distributed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

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

Season	Variable	Records	N	Correlation	*p*-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

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

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

		UDOI		Relatedness		Sex	
Season	N	Partial corr	*p*-value	Partial corr	*p*-value	Partial corr	*p*-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

508 *Relatedness among preferred associates*

509 We identified 18 (of 136 total) pairs of preferred associates, i.e., dyads
510 with AIs that were significantly higher than other dyads in the community. Of
511 these preferred associates, we were able to determine relatedness for 11 (91
512 total dyads with data for association and relatedness). Our logistic regression
513 model revealed that relatedness did not predict whether a pair of individuals
514 became preferred associates (coefficient = 0.087, p = 0.41) and thus did not
515 support prediction P2.1.

516

517 **Discussion**

518 Results from this study illustrate complex relationships among social
519 association, space use, and kinship in wild black-and-white ruffed lemurs,
520 patterns that—while unusual for primates—are well aligned with much of the
521 broader mammalian literature. We found that ruffed lemur social associations
522 varied immensely, ranging from no association between some individuals to
523 dyads observed together more than 75% of the time. From a community
524 perspective, the social network was sparse, with weak associations (AIs) being
525 common. Similarly, home range overlap was minimal and average relatedness
526 among community members was low. These patterns were consistent throughout
527 the year and across reproductive seasons. Together, these and earlier lines of
528 evidence (e.g., Baden, 2011; Baden et al., 2016) can be used to characterize
529 ruffed lemurs as having a spatiotemporally dispersed fission-fusion social
530 organization with weak social and kinship ties.

Kin selection theory (Hamilton, 1964) has long been invoked to explain the social preferences observed among mammals (e.g., Archie et al., 2006; Frère et al., 2010; Godde et al., 2015; Smith, 2014; Wahaj et al., 2004), particularly in primates (reviewed in Langergraber, 2012; Silk, 2002). In this study, however, we found no evidence that kinship structured either spatial overlap or social association overall in the community. In contrast to other fission-fusion species exhibiting similar patterns (Carter et al. 2013; Best et al. 2014), we further found that relatedness did not predict social preference. Instead, the closest social ties in the community appear to occur primarily between females and their preferred—and often unrelated—male social partners, followed by mothers and their pre-dispersal-aged subadult and adult offspring. Nevertheless, although fewer than ten percent (8.8%) of adult dyads within the community were genetic relatives, nearly three-quarters of adult females (85.7%) and all of adult males (100%) were closely related to at least one, and up to as many as three other same-sex relative(s). Thus, while our relatedness estimates suggest that ruffed lemur communities include both kin and non-kin, and that preferred associates are sometimes close relatives, kin are not forming spatial or social networks across the larger communal range. These patterns contrast with the spatially structured matrilines described in *Microcebus murinus* (Eberle & Kappeler, 2006; Radespiel, Lutermann, Schmelting, Bruford, & Zimmermann, 2003), the only other communally breeding strepsirrhine. Some authors have used this model to hypothesize that spatially structured kin networks have, at least in part, facilitated the evolution of cooperative infant care (Eberle & Kappeler, 2006). Cooperative

554 or communal breeding is exceedingly rare among primates (Tecot et al. 2013).
555 Only three nonhuman primates engage in this behavior: callitrichines (marmosets
556 and tamarins), cheirogaleids (mouse lemurs), and *Varecia* (Baden, Raboin,
557 Tecot, n.d.). Like cheirogaleids, callitrichines also rely on close relatives to share
558 the burden of infant care (reviewed in Erb & Porter 2017). *Varecia* are the only
559 group that does not rely on close relatives for care (Baden et al., 2013), thereby
560 distinguishing *Varecia*'s infant care strategies from other cooperatively breeding
561 nonhuman primates.

562 These results build on growing evidence that space use is an important
563 predictor of social association—perhaps moreso than kinship—particularly in
564 taxa characterized by high fission-fusion dynamics (Best et al., 2014; K. D. Carter
565 et al., 2013; Frère et al., 2010; Strickland et al., 2014). Indeed, for two individuals
566 to interact they must be in relatively close physical proximity (Farine 2015). For
567 most animals, this means that social associations are therefore shaped by their
568 movement decisions (Emlen and Oring 1977; Farine et al. 2016; Bonnell et al.
569 2017), which are, in turn, influenced by aspects of their physical environment
570 (e.g., habitat structure, natural and/or anthropogenic barriers, resource
571 availability and distribution; reviewed in He et al. 2019). Among these
572 environmental variables, resource availability and distribution play a fundamental
573 role in shaping the space use of animals (e.g., Brown and Orians 1970; Clutton-
574 Brock and Harvey 1977) and by extension, their patterns of inter-individual
575 spatial proximity (e.g., Minta 1992; Croft et al. 2011) and social relationships

576 (e.g., Sterck et al. 1997; Bejder, Fletcher & Brager 1998; Wolf et al. 2007; Carter
577 et al. 2009).

578 To this point, we found that while home range overlap explained most of
579 the variation seen in social association in ruffed lemurs, some variation remained
580 unaccounted for, suggesting that other social, ecological, and biological factors
581 must also be at play. However, it is possible that even weak or infrequent social
582 associations may facilitate cooperative resource defense against other
583 frugivorous competitors. For instance, ruffed lemurs actively defend fruit-bearing
584 trees against larger brown lemur (Genus *Eulemur*) groups for days or even
585 weeks during the resource scarce austral winter (Baden, personal observation).
586 Perhaps social association during these times better equips otherwise solitary
587 individuals to defend valuable fruit resources against interspecific competitors.
588 Under this scenario, we would predict higher AIs during resource scarce
589 seasons, periods that correspond primarily with mating/gestation, but also
590 birth/lactation seasons. However, AIs were lowest in the nonbreeding, resource
591 abundant periods (though not significantly so), lending minimal support for this
592 hypothesis. It is possible, however, that home range overlap as measured by
593 UDOIs was insufficient to characterize the spatiotemporal component of
594 associations at highly contested resources. Future analyses may therefore
595 benefit from a more nuanced investigation of the spatially explicit role valuable
596 resources play in the social associations of this species.

597 In addition, communal breeding plays an important role in female
598 reproductive success in this species (Baden et al., 2013) and might also be

important in driving social preferences. For instance, recent work suggests social networks in guppies may be structured by the propensity for non-kin to cooperate (Croft et al., 2009), which could lead to the maintenance of cooperation in the absence of kin assortment (Fletcher & Doebeli, 2009). These lines of research offer exciting opportunities to better understand the myriad factors shaping social preferences in fission-fusion species.

Nevertheless, shared space use does not always necessitate social association. In this study, we found that not all dyads with a high degree of home range overlap were close social associates. Indeed, many dyads with nonzero spatial overlap were never observed together. Similar patterns have been observed in dolphins, giraffes, and water dragons, wherein subjects did not associate, despite sharing complete or near complete home range overlap (i.e., 'social avoidance' in dolphins: Frère et al., 2010; giraffes: K. D. Carter et al., 2013; water dragons: Strickland et al., 2014, 2017). In such cases, individuals may actively and consistently avoid one another, despite the spatio-temporal potential for repeated interactions (reviewed in Strickland et al. 2017). Like predator avoidance, social avoidance can be costly. Thus, in future studies, it will be critical to simultaneously consider the consequences of both social attraction and avoidance when studying the evolution of sociality.

Together, these and earlier results raise important questions related to causation. What motivates social association? Are individuals that bias their time toward overlapping areas simply more likely to associate? Or, in cases where patterns of spatial overlap and social association do not align, is there some

additional force shaping these spatial and social decisions? Evaluating these and other alternatives require further investigation.

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