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

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ABSTRACT

Several primates exhibit fission-fusion social dynamics, yet the factors shaping 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 using Mantel tests and MRQAP. 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. 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 among members of this species.

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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 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 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 and/or strength of females' social connections 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*

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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

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knowledge (McComb, Moss, Durant, Baker, & Sayialel, 2001; Salpeteur et al., 2015). However, social integration has also been shown to have strong direct fitness consequences between nonrelatives (Baden, Wright, Louis, & Bradley, 2013; Cameron et al., 2009; G. G. Carter & Wilkinson, 2015; Riehl, 2011), suggesting that social bonds can evolve based on these 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 ties.

One complicating factor in determining whether and how kinship shapes social bonds 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,

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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 rare, 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).

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

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(i.e., both sexes disperse: Baden et al., 2014), communities nevertheless contain networks of closely related kin (e.g, Baden, 2011; Baden et al., 2013). Taken together, these lines of evidence suggest that 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 investigate the relative influences of space use and kinship on the strength of associations amongst members of a black-and-white ruffed lemur (*Varecia variegata*) community. Specifically, we quantify dyadic measures of association, home range overlap, and genetic relatedness to address the overarching question: What influences social association in ruffed lemurs?

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). Animals were collared under veterinary supervision following a strict protocol (Glander, 1993). Nineteen infants were born in the 2008

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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.

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

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

Genetic sampling

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

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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).

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We used SOCPROG 2.9 (Whitehead, 2009) to calculate association indices between all pairs of individuals using the "simple ratio" index, which quantifies the proportion of time that two individuals are observed together relative to their total observation time overall. This index is appropriate when individuals are equally likely to be correctly identified (Cairns & Schwager, 1987; Ginsberg & Young, 1992; Whitehead, 2008), which is the case for this population. Given that subgroup composition in this community changes 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 included 8 adult females and 9 adult males 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).

Spatial overlap

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

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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 UDs 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 µl
268 consisting of 2 µl template, 12.5 µl Qiagen HotStar Taq Master Mix, and 10 µM 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),

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

Correlations among association strengths, spatial overlap, and relatedness

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

Quantifying relatedness among dyads with "preferred" association strengths or spatial overlap

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

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

RESULTS

Association strength and spatial overlap

The average overall association index (AI) was 0.05 ± 0.03 (Baden et al., 2016). We observed similar mean AIs in each of the three reproductive seasons (nonbreeding = 0.04 ± 0.02; mating/gestation = 0.06 ± 0.03; birth/lactation = 0.07 ± 0.03). Within seasons, however, individuals varied substantially in their AIs. Average individual 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).

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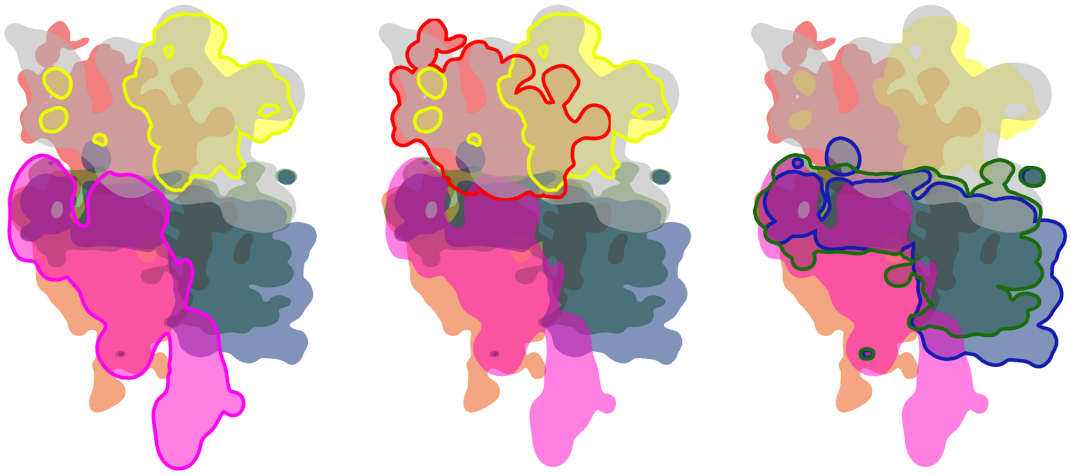
339 Average home range overlap (UDOI) was 0.211 ± 0.357. Some dyads did
340 not overlap at all (UDOI = 0), while the maximum UDOI observed was 1.895
341 (Figure 1). As with AIs, we observed similar mean UDOIs in each of the three
342 reproductive seasons (nonbreeding = 0.17 ± 0.27; mating/gestation =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



344

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

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Table 1. Summary of association indices, utilization distribution overlap indices (UDOIs), and relatedness 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

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

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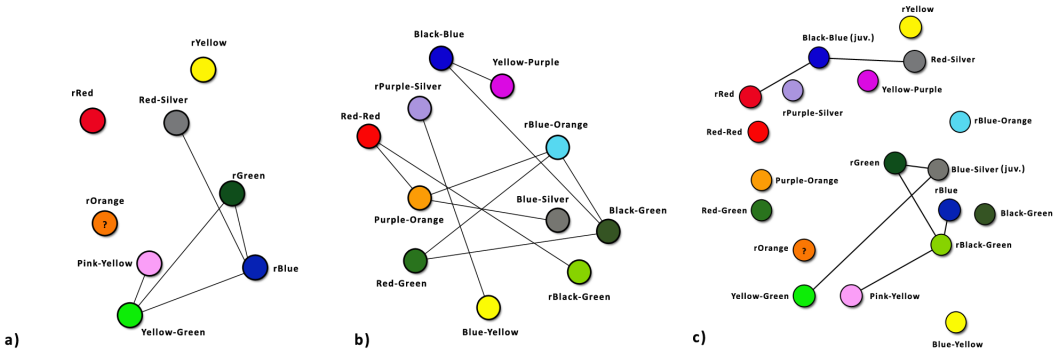
366 dyadic r-value calculations included all possible dyads (n = 703 dyads), as all
367 individuals could be compared at 5 or more loci. Average pairwise relatedness
368 among adults within the community was -0.06 ± 0.02 and ranged from -0.72 to
369 0.65 (Table 1; Figure 2).



370

371 *Figure 2. Pairwise genetic relatedness (r >= 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 << 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

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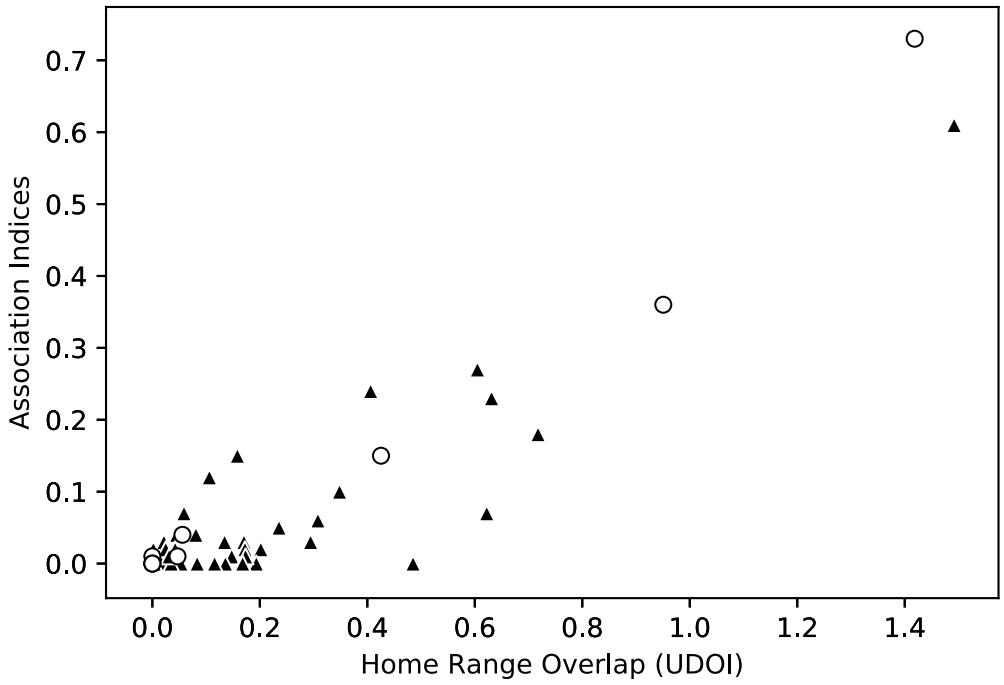
386 positive, while kinship and sex were never significantly correlated with AI (Table
387 3).



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, UDOIs range from 0 (no overlap)*
391 *to 1 (complete overlap); values of >1 are possible if both UDs 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>=0.25); black triangles*
394 *indicate non-kin (r<0.25).*

395

396

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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.

Table 3. Results from a multiple regression quadratic assignment procedure (MRQAP) investigating the partial 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

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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 $R_{xAI_non\text{-}preferred}$
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 $R_{xUDOI_non\text{-}preferred}$ = -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

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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 matrilines 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

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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.

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One possibility is that even weak or infrequent social associations may facilitate cooperative resource defense against other frugivorous competitors. For instance, ruffed lemurs actively defend fruit-bearing trees against larger brown lemur (Genus *Eulemur*) groups for days or even weeks during the resource scarce austral winter (Baden, personal observation). Perhaps social association during these times better equips otherwise solitary individuals to defend valuable fruit resources against interspecific competitors. If this was the case, one might expect higher AIs during resource scarce seasons, periods that correspond primarily with mating/gestation, but also birth/lactation seasons. AIs were lowest in the nonbreeding, resource abundant periods, though not significantly so, lending minimal support for this hypothesis. In addition, communal breeding plays an important role in female 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.

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