RESEARCH ARTICLE

Resource Seasonality and Reproduction Predict Fission–Fusion Dynamics in Black-and-White Ruffed Lemurs (*Varecia variegata*)

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Ruffed lemurs (genus *Varecia*) are often described as having a flexible social organization, such that both cohesive (low fission–fusion dynamics) and fluid (high fission–fusion dynamics) grouping patterns have been observed. In ruffed lemur communities with high fission–fusion dynamics, group members vary in their temporal and spatial dispersion throughout a communally defended territory. These patterns have been likened to those observed in several haplorrhine species that exhibit the most fluid types of fission–fusion social organization (e.g., *Pan* and *Ateles*). To substantiate and further refine these claims, we describe the fission–fusion dynamics of a black-and-white ruffed lemur (*Varecia variegata*) community at Mangevo, an undisturbed primary rainforest site in Ranomafana National Park, Madagascar. We collected instantaneous group scan samples from August 2007–December 2008 (4,044 observation hours) to study and characterize patterns of subgroup size, composition, cohesion, and social association. In 16 consecutive months, we never found all members of the community together. In fact, individuals spent nearly half of their time alone. Subgroups were small, cohesive, and typically of mixed-sex composition. Mixed-sex subgroups were significantly larger, less cohesive, and more common than either male-only or female-only subgroups. Subgroup dynamics were related to shifts in climate, phenology of preferred fruit species, and female reproductive state. On average, association indices were low. Males and females were equally gregarious; however, adult male–male associations were significantly weaker than any other association type. Results presented herein document striking differences in fission–fusion dynamics between black-and-white ruffed lemurs and haplorrhines, while also demonstrating many broad-scale similarities to haplorrhine taxa that possess the most fluid fission–fusion societies. Am. J. Primatol. 78:256–279, 2016.   © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

Gregariousness affords both costs and benefits to group-living primates [Alexander, 1974; Majolo et al., 2008; van Schaik, 1989]. Group size, in particular, is considered among the most important factors modulating behavior and individual fitness [Janson & Goldsmith, 1995; Koenig, 2002; Sterck et al., 1997; van Schaik, 1983; Wrangham, 1980]. As group size increases, individuals may benefit from improved success in intergroup contests over access to food resources [Janson & van Schaik, 1988; van Schaik, 1989; Wrangham, 1980], and reduced predation pressure [Hill & Lee, 1998; Sterck et al., 1997; van Schaik, 1983]; however, they may simultaneously face greater intragroup feeding competition [Alexander, 1974; Clutton-Brock & Harvey, 1977; Isbell, 1991; Janson & van Schaik, 1988; Terborgh &

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Janson, 1986; van Schaik, 1989], increased conspic-uousness to predators [e.g., Stanford, 1998] or to infanticidal males [e.g., Crockett and Janson, 2000], higher physiological stress [Pride, 2005; Snaith et al., 2008], and greater susceptibility to disease [Caillaud et al., 2013; Nunn & Heymann, 2005; Rifkin et al., 2012]. Group size should thus reflect an optimization of the benefits and costs of group living, primarily in relation to two key factors: resource competition (over food or mates) and predator avoidance [Terborgh & Janson, 1986]. Local selective pressures can change the benefit-to-cost ratio of gregariousness, and can influence the size and composition of social groups; in fact, optimal group size may change with time, even within the same population [van Schaik & van Hooff, 1983].

In some species, group members are able to individually optimize the costs and benefits of group living via a strategy known as "fission–fusion" [*sensu* Kummer, 1971]. In these taxa, individuals form socially and geographically circumscribed unit groups (i.e., communities) within which members associate in temporary, flexible subunits (i.e., parties or subgroups) that vary in size, cohesion, member-ship, and duration [e.g., Mitani et al., 2002b]. Although the precise social and ecological factors that promote fission–fusion social dynamics are not fully understood, this behavior is thought to function primarily to minimize within-group competition over access to food and mates [Chapman et al., 1995; Mitani et al., 2002a and references therein]. Specifi-cally, subgroup size is often closely tied to the availability of high-quality food resources, particu-larly ripe fruit [Asensio et al., 2009; Chapman et al., 1995; Symington, 1987, 1988b and references therein]. For example, groups fission and subgroups tend to be smaller and/or less cohesive when resources are scarce [e.g, Aureli & Schaffner, 2008; Anderson et al., 2002; Boesch, 1996; Chapman et al., 1995; Doran, 1997; Ghiglieri, 1984; Klein & Klein, 1977; Matsumoto-Oda et al., 1998; Mitani et al., 2002a; Morland, 1991a; Newton-Fisher et al., 2000; Shimooka, 2003; Symington, 1988a, 1990; Vasey, 2006; Wrangham, 1977, 1980; Wrangham et al., 1992, 1996; but see Stanford et al., 1994; Boesch, 1996; Hashimoto et al., 2001, 2003], when foods are patchily distributed (i.e., non-defensible), or when patches are small [Chapman, 1990a,b; Chapman et al., 1995; de Moraes et al., 1998; Isabirye-Basuta, 1988; Klein & Klein, 1977; Newton-Fisher et al., 2000; Potts et al., 2011; Shimooka, 2003; Stevenson et al., 1998; Symington, 1988b, 1990; Vasey, 2000; White & Wrangham, 1988; Wittiger & Boesch, 2013; Wrangham, 1977, 1980, 1986].

In addition, variation in subgroup size has been attributed to demographic factors (e.g., community size, sex ratio [Boesch, 1996; Goodall, 1986; Newton-Fisher, 1999; Newton-Fisher et al., 2000]) and behavioral context (e.g., cooperative hunting or

territorial patrols [Boesch & Boesch, 1989; Wallace, 2008]), as well as infant socialization [Chapman et al., 1994; Newton-Fisher, 1999; Williams et al., 2002] and female reproductive state [Anderson et al., 2002; Chapman, 1990a; Boesch & Boesch-Acher-mann, 2000; Goodall, 1986; Hashimoto et al., 2001; Matsumoto-Oda, 1999; Matsumoto-Oda et al., 1998; Mitani et al., 2002a; Sakura, 1994; Shimooka, 2003; Stanford et al., 1994; Symington, 1987; Wrangham, 2000]). Mixed-sex subgroups are typically larger when estrus/cycling females are present. Non-cycling adult females (i.e., those that are pregnant, lactating, or post-reproductive) are less commonly observed in large bisexual parties [Matsumoto-Oda, 1999], and instead, pregnant females tend to be less social [Goodall, 1986; Nishida, 1990], especially just before parturition [Pusey et al., 2008]. Likewise, lactating females generally spend more time alone [Goodall, 1986; Hasegawa, 1990; Kawanaka, 1984 Sakura, 1994; Uehara, 1981; Wrangham & Smuts, 1980; but see Shimooka, 2003; Vasey, 2007] or in small subgroups with other lactating females [Sakura, 1994; Slater et al., 2009].

Because primate social organization has histori-cally been classified into a handful of modal catego-ries, only primates exhibiting the most extreme forms of fission–fusion have typically been classified as having a "fission–fusion social organization" [Aureli et al., 2008; Clutton-Brock & Harvey, 1977; Di Fiore & Rendall, 1994; Kappeler, 1997; Strier, 1994]. For this reason, our knowledge of primate fission–fusion stems primarily from studies of chimpanzees (*Pan troglodytes*) [Boesch & Boesch-Achermann, 2000; Mitani et al., 2002a,b; Nishida & Hiraiwa-Hasegawa, 1987], bonobos (*P. paniscus*) [Furuichi, 2009; Hohmann & Fruth, 2002; Stumpf, 2011], and spider monkeys [*Ateles* spp.: Chapman et al., 1995; Di Fiore et al., 2011; Symington, 1990]. Convergent patterns of fission–fusion among these taxa suggest that similar social systems have evolved in response to similar selection pressures in distantly related taxa. However, with increased knowledge of individual ranging patterns, it is becoming clear that flexible spatiotemporal grouping patterns in pri-mates and other vertebrates are more common—and more complex—than generally recognized [e.g., Aureli et al., 2008; Kinzey & Cunningham, 1994; Struhsaker & Leland, 1979; Sussman & Garber, 2011]. In fact, fission–fusion dynamics [*sensu* Aureli et al., 2008] can be quantified in any primate group that varies, even minimally, in terms of its size, membership, and spatial cohesion through time (e.g., brown lemurs [Overdorff et al., 2003; Toborowsky, 2008], capuchins [Lynch-Alfaro, 2007], geladas [Snyder-Mackler et al., 2012], howler monkeys [Bezanson et al., 2008], humans [Marlowe, 2005], macaques [Ménard, 2002], muriquis [Coles et al., 2012], ring-tailed lemurs [L. Kelley, pers. comm.], saki monkeys [Veiga et al., 2006]; snub-nosed

monkeys [Ren et al., 2012], uakaris [Bowler & Bodmer, 2009; Bowler et al., 2012]).

In this study, we characterize the nature of fission–fusion dynamics in a population of black-and-white ruffed lemurs (*Varecia variegata*). Ruffed lemurs are relatively large-bodied [2.5–4.8 kg; Baden et al., 2008], arboreal frugivores endemic to the eastern rainforests of Madagascar [Baden, 2011; Balko, 1998; Morland, 1991a; Ratsimbazafy, 2002; Rigamonti, 1993; Vasey, 2000]. While initially described as living in cohesive, pair-bonded groups [Petter et al., 1977; Pollock, 1979; White, 1991], nearly all subsequent long-term studies describe ruffed lemurs as living in groups characterized by high fission–fusion social dynamics [Baden, 2011; Morland, 1991a,b; Rigamonti, 1993; Vasey, 2006; but see Balko, 1998; Britt, 1997; Ratsimbazafy, 2002]. Groups or "communities" typically range in size between 11 and 31 individuals [Baden, 2011; Morland, 1991a,b; Vasey, 2006], though members are rarely if ever all seen together in the same place at the same time. Aspects of their fission–fusion dynamics—including range use, spatial associations, and affiliative interactions—vary according to season, resource availability, and female reproductive state [Morland, 1991a,b; Rigamonti, 1993; Vasey, 2006], and their associations have been described as "female-bonded" [Morland, 1991a]. These foundational studies of fission–fusion sociality in the strepsirrhine genus *Varecia* have demonstrated some remarkable similarities with haplorrhine taxa that exhibit the most extreme forms of fission–fusion sociality (e.g., chimpanzees, bonobos, and spider monkeys). To substantiate and further refine these claims, we employ multivariate modeling to gauge the relative influence of various social and ecological factors thought to impact subgroup size and cohesion. We report on subgroup size, type, cohesion, and duration, and describe patterns of association within one communal *V. variegata* territory. Further, we evaluate whether and how ruffed lemur fission–fusion dynamics vary with seasonal shifts in climate, fruit availability, and reproductive state. Finally, to assess species and population parallels and differences, we couch our results in a larger comparative context of primate fission–fusion dynamics.

Study Site and Subjects

Data were collected from one *V. variegata* community at Mangevo bushcamp in Ranomafana National Park, Madagascar (RNP) for 16 months (August–December 2007; February–December 2008). Mangevo [21°22′60″S, 47°28′0″E] is a mid elevation (660–1,200 m) primary rainforest site within the southeastern parcel of RNP, containing 435 km^2 of continuous montane rainforest located in the southeastern escarpment of Madagascar's central high plateau [21°02′–21°25′S and 47°18′–47° 37′E; Wright et al., 2012].

All members of the Mangevo ruffed lemur community were habituated to human observers and were individually identified via radio-collars and/or unique collar-tag combinations prior to the study. Animals were collared under veterinary supervision following a strict protocol previously outlined [Glander, 1993]. At the time of the study, the community included 24 adults and subadults (8 adult females, 11 adult males, 5 subadult males). Nineteen infants were born in the 2008 birth season and were present from October to December 2008, when the study ended. Of the study subjects, 5 females and 3 males were radio-collared and targeted for regular follows. Individuals with collar-tags (but no radio-collars, $n = 16$) were opportunistically targeted for focal follows. Sampling efforts resulted in a total of 4,044 focal observation hours.

Research protocols were in compliance with and permission was granted by Stony Brook University IACUC #2005-20081449 and Madagascar's National Parks (ANGAP/MNP), and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Data Collection

Two teams of four observers each conducted dawn-to-dusk follows on focal individuals, (i.e., two animals were followed daily). A focal animal was located at the beginning of each observation period via radio-telemetry. Only independent individuals (adults and subadults) were targeted for follows. New focals were selected daily. Focals were never sampled on consecutive days and every effort was made to follow all focals at least once per month. If an individual with a collar-tag was located in association with a radio-collared focal individual prior to 10:00 h, this individual became the new focal for that observation period. Observation periods ranged in duration between 8 and 11 hr depending on seasonal differences in day length and time needed to locate animals at dawn.

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. Subgroups were defined as all independent individuals (i.e., adults and subadults) within a 50 m radius of the approximate subgroup center that exhibited coordinated behavior and travel (i.e., traveling in the same direction). This threshold was chosen because: (i) four observers could reliably detect and differentiate animals within 50 m and (ii) subgroup members within this radius were assumed

to be in visual contact with each other as individuals visible to the observer were presumably also visible to each other [Lehmann & Boesch, 2004]. Our subgroup definition is similar to that described by Coles et al. [2012], in that it combined both a *general* spatial criterion [i.e., all individuals in sight: Boesch, 1996; Chapman, 1990a; Itoh & Nishida, 2007] and a *specific* spatial criterion [i.e., all individuals within a defined radius: Morgan, 2007; Newton-Fisher et al., 2000]. We also noted, *ad libitum*, the number, identity, and distance of individuals that were observed outside of the 50 m radius and monitored their individual behavior (e.g., whether the animal approached, retreated from, or exhibited coordinated travel with the subgroup being studied) while in sight. These instances were rare, and generally comprised a solitary individual traveling past the subgroup at distances of at least 100 m. However, in cases where animals spent considerable time (i.e., ≥30 min) traveling in the same direction as and/or coordinating activity with the subgroup being followed, these animals were, *post hoc*, considered part of the subgroup, and were included in estimates of subgroup size, composition, and cohesion.

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 five activity states: (1) feed/forage (to search for, procure, ingest, or chew any food item); (2) travel (movement from one location to another, excluding changing position within a patch during feeding/foraging); (3) rest (stationary with no apparent activity); (4) social (active interaction between ≥2 individuals); and (5) other (e.g., self-groom). If a social interaction occurred during any of the other four activity categories (e.g., an agonistic interaction during a feeding bout), "social" was recorded. Subgroup type (i.e., the sex composition of subgroups: female only, male only, mixed sex) was assigned *post hoc* according to the composition of subgroups at each 5 min scan. Subgroup fission events were recorded when ≥1 individual(s) were absent from more than two consecutive group scans; fusion events were recorded when ≥1 individual(s) not previously belonging to the subgroup were found in association with another subgroup member during a group scan. With these methods, we recorded a total of 40,840 group scans and 2,514 changes in subgroup size and/or composition (fission and/or fusion events).

Because phenological patterns of fruit abundance and scarcity in Madagascar often closely correlate with climatic changes in temperature and rainfall [Dewar & Richard, 2007; Hemingway, 1996, 1998; Meyers & Wright, 1993; Overdorff, 1993], we collected daily measurements of total rainfall (mm),

and mean, minimum, and maximum temperatures (C°). Throughout the study, we also monitored fruiting productivity and female reproductive state as these have previously been related to patterns of fission–fusion dynamics. Figure 1 illustrates the correspondence between climate, fruit availability, and female reproductive state during the study period. Because females bore young during the birth season in late 2008, but not in 2007, data were collected during early lactation (October–December 2008), but not during mid to late lactation (January–February/March 2008).

We estimated fruit availability from 637 trees and lianas found within 12 botanical plots ($10 \times 50 \text{ m}^2$ or 500 m^2) established evenly throughout the communal home range (87.8 ha; [Baden, 2011; Baden & Gerber, in prep]). We monitored only those species known to comprise the top 25 preferred *Varecia* food resources [as per Baden & Gerber, in prep; Balko, 1998]. Within each plot, we identified the following information for each stem ≥5 cm diameter at breast height (DBH): species identity, position (x, y) relative to plot origin, DBH, height, crown height, and crown diameter. Plants were monitored during one week per month. Each tree was assigned a percentage score for each of four phenophases (flower buds, flowers, unripe fruit, ripe fruit), representing the estimated crown coverage. Because all four phenophases occupy the same physical space within the crown, the sum of the four scores did not exceed 100%. From these records, we calculated an estimate of monthly fruit availability (%) by summing the percent ripe and unripe fruits for each tree and then averaging across species.

Female reproductive state was noted at the beginning of each observation period. Ruffed lemurs are strict seasonal breeders and exhibit clear signs of behavioral and vaginal estrus [Brockman et al., 1987; Foerg, 1982; Morland, 1993; Pereira et al., 1988]. Thus, we were able to easily assess female reproductive state as one of three broad reproductive categories during our study: anestrus, gestation, and lactation.

Data Analyses
Characterizing ruffed lemur fission–fusion dynamics
From the full dataset (40,840 scans), we calculated descriptive statistics related to fission–fusion social dynamics within the community, including the rate of subgroup fissions and fusions, subgroup size, and subgroup cohesion. To make our data comparable to those from other studies and taxa, we present subgroup size as both absolute and relative measures (i.e., subgroup size expressed as a percentage of total group size *sensu* Boesch [1996]). We excluded the first scan in each observation period when calculating rates of fissions and fusions, as
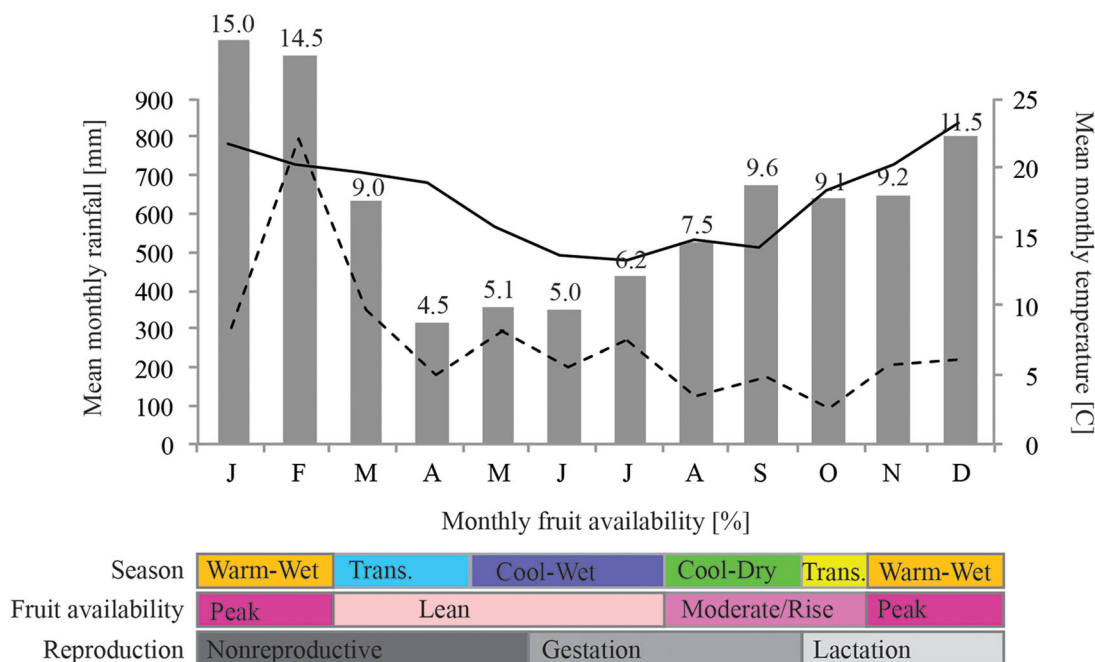
Fig. 1. Correspondence of climate, fruit availability, and reproductive state during the study period. Dashed line represents rainfall; solid line represents temperature. Note: no infants were born in 2007, thus January–June 2008 were considered non-reproductive months. In other years, some of these months would be a continuation of lactation.

subgroup size and composition prior to the first scan was unknown.

Sampling was biased toward radio-collared females. We, therefore, analyzed only a subset of our data to ascertain subgroup type and association patterns. Scans containing unknown individuals (i.e., animals with neither radio-collars nor collar-tags) were removed and data were then divided by month according to whether the focal individual was male or female. We then randomized the point scans and selected X scans to include in the dataset for each sex, where X is equal to 90% of the point scans for the sex with the fewest scans in a given month. For example, in April 2008, there were 2,098 female focal scans and 789 male focal scans. We, therefore, randomly selected 1,420 point scans from April, such that we included 710 focal male scans (90% of 789, the smaller number) and 710 focal female scans in the subsampled dataset. This procedure resulted in a total of 11,784 point scans for inclusion in our analysis targeting equal numbers of males and females in each month. From this subsampled dataset, we calculated descriptive statistics for subgroup size, type, and sex ratio. We report means $\pm$ standard deviations.

Characterizing patterns of association

We used Socprog 2.5 [Whitehead, 2009] to calculate association indices between pairs of individuals using the "simple ratio" index, which is appropriate if individuals are equally likely to be

correctly identified [Cairns & Schwager, 1987; Ginsberg & Young, 1992; Whitehead, 2008]. The simple ratio index is defined as

$$\frac{x}{x + y_{AB} + y_A + y_B}, \qquad (1)$$

where $x =$ the number of sampling periods in which individuals A and B were observed/associated within a given subgroup, $y_{AB} =$ the number of sampling periods in which A and B were identified but not associated, $y_A =$ the number of sampling periods in which only A was identified, and $y_B =$ the number of sampling periods in which only B was identified. Because subgroup composition changed, on average, every 90 min, we set sampling periods to 6 hr to reduce autocorrelation among periods. We removed individuals observed in fewer than 10 sampling periods.

To test for sex differences in association, we performed a Mantel test implemented in Socprog 2.5 [Whitehead, 2009]. The Mantel test correlates the matrix of association indices and a 1:0 matrix indicating whether or not members of a pair are the same sex, and compares that value to a distribution of values calculated by randomly permuting the sexes of individuals, allowing the calculation of statistical significance [Mantel, 1967; Schnell et al. 1985; Whitehead, 2008]. We increased the number of permutations until P values stabilized (n = 10,000). Tests were two-tailed and alpha was set at 0.05.

Factors predicting subgroup size and cohesion

We constructed linear mixed models (LMM) and generalized linear mixed models (GLMM) to assess factors influencing subgroup cohesion and subgroup size, respectively. We performed two analyses for each of these dependent variables. One model contained two climate variables as predictors, rainfall and temperature (as a proxy for fruit availability). These climate variables were the first two components generated from a principal components analysis (PCA). The PCA was based on a covariation matrix and was performed using the princomp function in R [R Development Core Team, 2014]. The second model contained fruit availability as a predictor. In addition, all models included the following fixed effects as predictor variables: female reproductive state, activity, and subgroup type. Models assessing subgroup cohesion also included subgroup size as a predictor as we were interested in subgroup cohesion patterns independent of subgroup size. Each model designated the focal individual and data collection day as random effects. We chose these two random effects because we used our point scans as samples in the analyses. Therefore, including these variables as random effects in the models allowed us to account for repeatedly measuring the same individual and the same day. This controlled for individual level variation, as well as uneven sampling among individuals. Similarly, including data collection day as a random effect accounted for multiple scans on the same day, many of which were associated with the same values for some variables (e.g., fruit availability, daily climate). We used the lmer and glmer functions in the R package lme4 [Bates et al., 2014] to conduct the LMM and GLMM models, respectively. For the GLMM models, "family" was set to poisson. The lmerTest package [Kuznetsova et al., 2014] was used to produce *P* values.

For each of the four full models, we used Akaike's Information Criterion corrected for small sample size (AICc) [Burnham & Anderson, 2002] to judge the combination of predictor variables that best fit the data. The model associated with the lowest AICc score was considered the best and other models within 2 AICc values were considered equally good [Burnham & Anderson, 2002]. This approach has several advantages over stepwise procedures [see Garamszegi, 2011 for a recent review]. Finally, we calculated the sum of AICc weights for each fixed effect to assess their relative importance. This metric varies from zero to one and fixed effects with higher values are more frequently present in the best models. Therefore, these predictors better explain the dependent variable. All AICc related metrics were calculated with the dredge function in the MuMin package for R [Bartoń, 2014].

RESULTS

Ruffed Lemur Fission–Fusion Dynamics

We never found all community members together in the same place at the same time; indeed, we never observed more than one-third of community members together in a subgroup. Focal individuals were solitary for nearly one-half (48%) of observations. During scans where at least two individuals were present, subgroups primarily comprised two or three individuals (mean $= 2.54 \pm 0.85$ s.d.; range $= 2$–7; $n = 21,219$; Fig. 2). Relative subgroup size within the community was equally low (mean $= 10.59\%$; range $= 8.33$–29.17%).

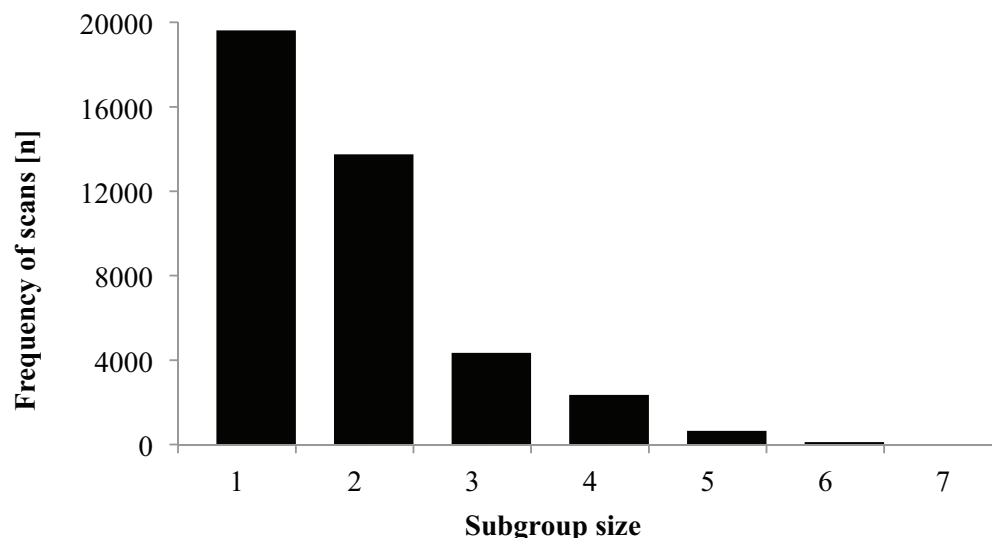Subgroups were typically cohesive, with an average group spread of 8.02 m ± 7.21 s.d.; however,

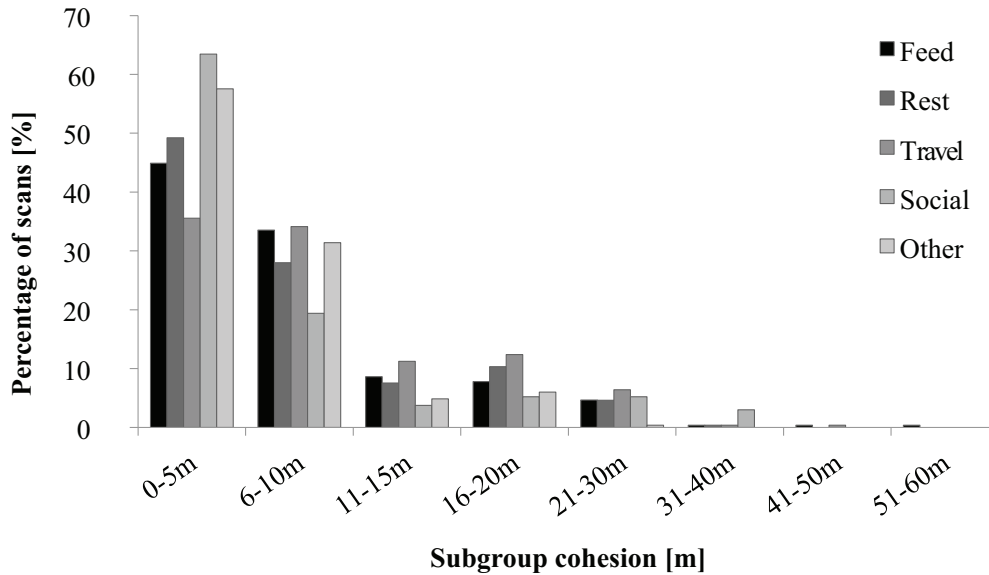Fig. 2. Frequency distribution of ruffed lemur subgroup sizes from 5 min time point scans (n = 40,840).

Fig. 3. Subgroup cohesion by activity type, as calculated from 5 min time point scans (n = 40,840).

group cohesion varied by activity type (range = 0–60 m; Fig. 3). Subgroups were most cohesive when members were engaged in social behaviors (mean$_{SOC}$ = 6.22 m ± 9.19 s.d.), followed by resting (mean$_{RST}$ = 7.70 m ± 7.17 s.d.), and feeding (mean$_{FD}$ = 8.24 m ± 6.96 s.d.). Subgroups were least cohesive during travel (mean$_{TRV}$ = 9.78 m ± 7.4 s.d.).

Subgroup size varied by subgroup type (Table I). When at least two individuals were present, mixed-sex subgroups were predominant (79.5%), followed by male-only (12.1%) and female-only (8.4%) subgroups. Mixed-sex subgroups were larger (2.57 ind. ± 0.82) than male-only (2.25 ind. ± 0.43) and female-only (2.08 ind. ± 0.28) subgroups (Table I), and sex ratios within mixed-sex subgroups were nearly equal (0.49 ± 0.38). Mixed-sex subgroups also reached larger maximum sizes than same-sex subgroups (Table I).

Males were only slightly more likely than females to be found in subgroups with at least one other individual (71% vs. 68%, respectively), and males and females were equally likely to be found in mixed-sex subgroups (62% vs. 61%, respectively).

On average, subgroup size and composition changed every 90 min. Fissions occurred every 173 min and fusions occurred every 174 min.

Social Association Patterns

Dyadic associations within the Mangevo community were generally weak, with values ranging between 0 (never associated) and 0.80 (11,765 scans; mean association index = 0.05 ± 0.03). When considering dyadic relationships among all independent community members (i.e., among adults and subadults), association indices did not differ significantly for same sex or mixed-sex dyads (Mantel test: $r = -0.08$, $P = 0.09$). However, subadult males exhibited unusually high association indices (mean = 0.09) and we noted that the association between two subadult males in particular—the highest observed association index, at 0.80—was likely inflating male association indices. We, therefore, reran analyses using adults only (11,171 records) and found adult male–male dyads exhibited significantly weaker association indices than adult female–female or mixed-sex dyads (Mantel test, $r = -0.15$, $P = 0.016$; mean adult male-male AI = 0.01 ± 0.01; mean adult male–female AI = 0.06 ± 0.04; mean adult female–male AI = 0.06 ± 0.03; mean adult female–female AI = 0.05 ± 0.02) (Fig. 4).

TABLE I. Variation in *Varecia variegata* Subgroup Size by Subgroup Type (Subsampled Dataset)

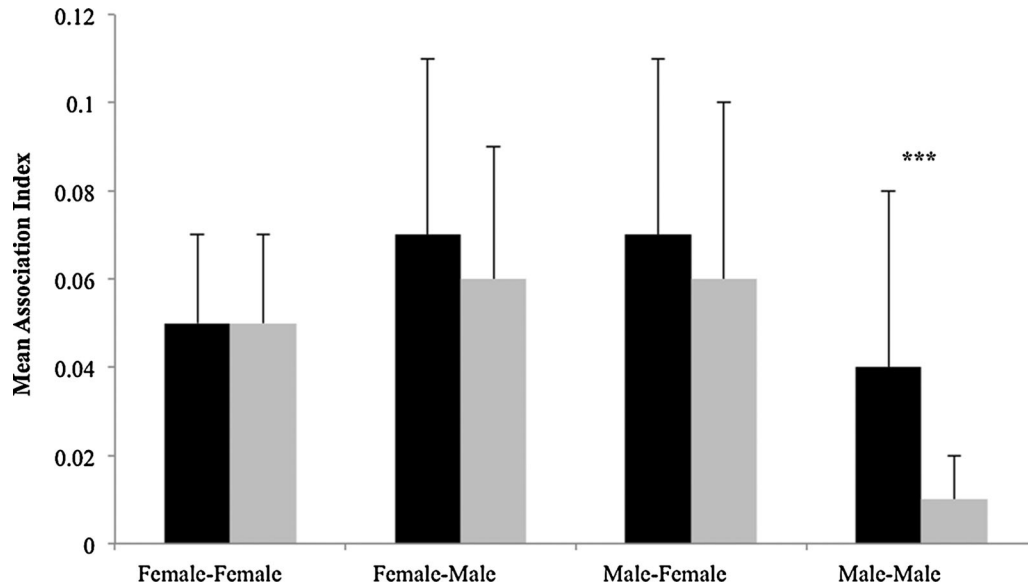| Sex composition	Scans (n)	% observations	Mean (±SD)	Min.	Max.
Solitary male	2,440	20.7	–	1	1
Solitary female	2,768	23.5	–	1	1
Males	796	6.8	1.31 ± 0.58	2	3
Females	553	4.7	1.18 ± 0.42	2	4
Mixed-sex	5,227	44.4	2.57 ± 0.82	2	6
Total	11,784				

Fig. 4. Association index values (means ± s.d.) according to subgroup type. Dark bars represent values for adults and subadults combined, while gray bars represent values for adults only. ***$P < 0.001$

Factors Predicting Subgroup Size and Cohesion

For the GLMM predicting subgroup size, which used climate variables as a proxy for fruit availability, a single model had the lowest AICc value. No other model was within 2 AIC values of this best model. This model contained all the predictors except for activity (Table II). Based on the sum of AICc weights, subgroup type and reproductive state were the most important predictors (values of 1.00 and 0.94, respectively) (Table III). The two climate variables exhibited moderately high values (0.83 and 0.75, respectively), and activity displayed a low value (0.16). This latter result suggests that subgroup size was only weakly related to activity. Smaller subgroups (solitary individuals) were associated with the early lactation period, as well as lower temperature and rainfall values (as loaded on the climate PCA axes). Larger subgroups were associated with mixed sex subgroups (Table I).

TABLE II. Results of Generalized Linear Mixed Model Predicting Subgroup Size Using Climate Variables as a Proxy for Fruit Availability. Full Model Results Are Presented Here

Fixed effect	Estimate	Std. error	z value	P
(Intercept)	0.756	0.041	18.66	<0.001
Climate_PCA1	−0.020	0.008	−2.41	0.016
Climate_PCA2	−0.022	0.010	−2.10	0.035
ReprodState_Lactation	−0.129	0.039	−3.34	0.001
ReprodState_Nonreproductive	−0.043	0.032	−1.36	0.174
Activity_Other	0.007	0.020	0.36	0.715
Activity_Rest	−0.001	0.010	−0.09	0.931
Activity_Social	0.106	0.050	2.11	0.035
Activity_Travel	−0.006	0.017	−0.34	0.732
SubGpType_MaleOnly	−0.087	0.044	−1.98	0.048
SubGpType_MixedSex	0.222	0.017	12.75	<0.001
SubGpType_SolitaryFemale	−0.684	0.019	−36.32	<0.001
SubGpType_SolitaryMale	−0.667	0.032	−20.56	<0.001

Model AICc = 83694.7; logLikelihood = −41832.34.
The model with the best AICc value (83691.5) did not contain the activity variable.
The focal individual and data collection day were used as random effects.
Gestation is the reference category for the Reproductive State variable. Feed/forage is the reference category for the activity variable.
Female only is the reference category for the Subgroup Type variable.
The P-value associated with each listed category indicates whether it is significantly different from the reference category noted in the footer, e.g., social is associated with lower group spread than feed/forage.

TABLE III. Relative Importance of Predictor Variables for Explaining Variation in Subgroup Size and Cohesion Based on the Sum of AICc Weights

Model	Climate PCA1	Climate PCA2	Fruit availability	Reproductive state	Sex composition	Activity state	Subgroup size
Predicting subgroup size[a]	0.83	0.75	–	0.94	1	0.16	–
Predicting subgroup size[b]	–	–	1	1	1	0.06	–
Predicting subgroup cohesion[a]	0.14	0.57	–	1	1	1	1
Predicting subgroup cohesion[b]	–	–	0.98	1	1	1	1

Note: The sum of AICc weights vary from zero to one.
[a]Model using climate variables as proxy for fruit availability.
[b]Model using phenological plots as proxy for fruit availability.

The GLMM predicting subgroup size that included fruit availability produced similar results. A single model had the lowest AICc value and contained all the predictors except for activity (no other model was within 2 values of this best model) (Table IV). Based on the sum of AICc weights, subgroup type, reproductive state, and fruit availability were the most important predictors (all exhibited a value of 1.00) (Table III). In contrast, activity displayed a value of 0.06. Again, smaller subgroup sizes were associated with the early lactation period, whereas larger subgroup sizes were associated with mixed-sex subgroups and higher fruit availability.

Our LMM predicting subgroup cohesion and including climate variables as a proxy for fruit availability generated two best models based on AICc. The model with the lowest AICc value (105316.4) contained all predictor variables except for climate PCA 1 (Table V). An equivalent model (AICc = 105316.9) contained all predictors except for either of the climate variables. Based on the sum of

AICc weights, subgroup type, subgroup size, reproductive state, and activity were the most important predictors (all exhibited values of 1.00) (Table III). Climate PCA 2 exhibited a moderate score, 0.57, and climate PCA 1 exhibited a low score 0.14. Greater subgroup cohesion was associated with the lactation period, as well as time spent resting and social. Reduced subgroup cohesion was associated with mixed sex. Finally, subgroup size was negatively related to subgroup cohesion.

Finally, our LMM predicting subgroup cohesion and using fruit availability produced a single best model based on AICc (no other model was within 2 values of this best model). This model contained all predictor variables (Table VI). Based on the sum of AICc weights, all the predictors were nearly equally important (Table III). All predictors exhibited a sum of AICc weight value of 1.00, except for fruit availability, which was 0.98. Greater subgroup cohesion was associated with the lactation period, as well as time spent resting and social. Higher fruit availability was also associated with greater

TABLE IV. Results of Generalized Linear Mixed Model Predicting Subgroup Size Using Fruit Availability From Botanical Plots. Full Model Results Are Presented Here. The *P* Value Associated With Each Listed Category Indicates Whether It is Significantly Different From the Reference Category Noted in the Footer, e.g., Social is Associated With Lower Group Spread Than Feed/Forage

Fixed effect	Estimate	Std. error	z value	P
(Intercept)	0.524	0.053	9.90	<0.001
TotalFruitAvailable	2.713	0.458	5.92	<0.001
ReprodState_Lactation	−0.125	0.032	−3.96	<0.001
ReprodState_Nonreproductive	0.016	0.028	0.57	0.572
Activity_Other	0.004	0.021	0.19	0.848
Activity_Rest	−0.002	0.011	−0.14	0.888
Activity_Social	0.089	0.060	1.48	0.139
Activity_Travel	−0.007	0.018	−0.40	0.689
SubGpType_MaleOnly	−0.112	0.046	−2.45	0.014
SubGpType_MixedSex	0.217	0.018	12.09	<0.001
SubGpType_SolitaryFemale	−0.681	0.020	−34.76	<0.001
SubGpType_SolitaryMale	−0.685	0.034	−19.87	<0.001

Model AICc = 76652.4; logLikelihood = −38312.22.
The model with the best AICc value (76646.9) did not contain the activity variable.
The focal individual and data collection day were used as random effects.
Gestation is the reference category for the Reproductive State variable.
Feed/forage is the reference category for the Activity variable. Female only is the reference category for the Subgroup Type variable.

TABLE V. Results of Linear Mixed Model Predicting Subgroup Cohesion Using Climate Variables as a Proxy for Fruit Availability. Full Model Results Are Presented Here. The P Value Associated with Each Listed Category Indicates Whether It is Significantly Different From the Reference Category Noted in the Footer, e.g., Social is Associated With Lower Group Spread than Feed/Forage

Fixed effect	Estimate	Std. error	t value	P
(Intercept)	0.081	0.754	0.11	0.914
Climate_PCA1	0.038	0.179	0.21	0.831
Climate_PCA2	0.435	0.224	1.94	0.054
ReprodState_Lactation	−1.943	0.809	−2.40	0.017
ReprodState_Nonreproductive	1.754	0.665	2.64	0.009
Activity_Other	−0.050	0.237	−0.21	0.832
Activity_Rest	−0.699	0.115	−6.08	<0.001
Activity_Social	−3.052	0.520	−5.87	<0.001
Activity_Travel	2.508	0.201	12.50	<0.001
SubGpType_MaleOnly	2.242	0.430	5.21	<0.001
SubGpType_MixedSex	1.361	0.171	7.97	<0.001
SubGpType_SolitaryFemale	4.970	1.144	4.34	<0.001
SubGpType_SolitaryMale	5.737	2.333	2.46	0.014
Subgroup size	2.637	0.081	32.51	<0.001

Model AICc = 105319.9; logLikelihood = −52642.94.
The model with the best AICc value (105316.4) did not contain Climate_PCA1.
The focal individual and data collection day were used as random effects.
Gestation is the reference category for the Reproductive State variable.
Feed/forage is the reference category for the Activity variable.
Female only is the reference category for the Subgroup Type variable.

subgroup cohesion values, though the P value was 0.08 in the full model. Finally, reduced subgroup size was associated with mixed sex subgroup types. Again, subgroup size was negatively related to subgroup cohesion.

DISCUSSION

Ruffed Lemur Fission Fusion Dynamics

Ruffed lemurs are often described as having a flexible social organization, such that both cohesive (low fission–fusion dynamics) and fluid grouping patterns (high fission–fusion dynamics) have been observed [reviewed in Vasey, 2003, 2006]. Results from this study demonstrate that, much like patterns characteristic of northern ruffed lemur populations [Morland, 1991a,b; Rigamonti, 1993; Vasey, 2006], members of the Mangevo community exhibit a high level of fission–fusion dynamics. In 16 consecutive months, we never found all members of the community together. Rather, community members regularly associated in subgroups that varied in size,

TABLE VI. Results of Linear Mixed Model Predicting Subgroup Cohesion and Using Fruit Availability from Botanical Plots as a Proxy for Fruit Availability. Full Model Results Are Presented Here. The P Value Associated With Each Listed Category Indicates Whether It is Significantly Different From the Reference Category Noted in the Footer, e.g., Social is Associated With Lower Group Spread than Feed/Forage

Fixed effect	Estimate	Std. error	t value	P
(Intercept)	1.961	1.116	1.76	0.080
TotalFruitAvailable	−19.180	10.910	−1.76	0.080
ReprodState_Lactation	−1.890	0.718	−2.63	0.009
ReprodState_Nonreproductive	1.573	0.628	2.50	0.013
Activity_Other	0.015	0.235	0.06	0.950
Activity_Rest	−0.581	0.120	−4.86	<0.001
Activity_Social	−2.769	0.607	−4.56	<0.001
Activity_Travel	2.511	0.206	12.18	<0.001
SubGpType_MaleOnly	2.058	0.439	4.69	<0.001
SubGpType_MixedSex	1.382	0.171	8.09	<0.001
SubGpType_SolitaryFemale	5.568	1.149	4.85	<0.001
SubGpType_SolitaryMale	5.596	2.294	2.44	0.015
Subgroup size	2.529	0.085	29.73	<0.001

Model AICc = 96050.5; logLikelihood = −48009.25
The focal individual and data collection day were used as random effects. Gestation is the reference category for the Reproductive State variable.
Feed/forage is the reference category for the Activity variable. Female only is the reference category for the Subgroup Type variable.

composition, and cohesion. On average, subgroup transitions (either fissions or fusions) occurred every 90 min and, much like previous studies of the species [Morland, 1991a,b; Ratsimbazafy, 2002], Mangevo community members spent nearly half of their time alone. When located with other community members, subgroups were generally small (2–7 individuals; 10.6% of community) and cohesive (within 8 m) and typically comprised only one or two subadult and/or adult individuals. Mixed-sex subgroups predominated, followed by male-only and female-only subgroups. Mixed-sex subgroups were also significantly larger and less cohesive than any other subgroup type. That said, with the exception of subadult males, who exhibited unusually strong patterns of association with each other—perhaps representing members of a single birth cohort—adult females appeared to be central to social associations within the community. Females interacted equally with both male and female community members, whereas adult males appeared to interact primarily with adult females. These findings parallel Morland's accounts from Nosy Mangabe [1991a,b], wherein the highest rates of interaction were found among immature age–sex classes and female–female dyads. Affiliative interactions between other age–sex combinations comprised only 15% of the total interactions observed, leading Morland [1991a] to conclude that ruffed lemurs exhibit a type of "female bonded fission–fusion." Social network analyses among members of the Mangevo ruffed lemur community are underway and will be used to test this hypothesis.

Compared to other primates for which fission–fusion has been quantified, ruffed lemur community size (range: 11–31 individuals) is smaller than that of many chimpanzee communities (e.g., Gombe, Ngogo, Taï), but similar in size to communities observed for bonobos, spider monkeys, and several other platyrrhines (e.g., muriquis, capuchins; Table VII). As is typical of haplorrhine taxa showing high fission–fusion dynamics, ruffed lemur subgroups varied frequently in size, composition, and cohesion. Subgroup duration observed in this study (90 min) was on the same order as in chimpanzees (17–126 min: Boesch [1996]; Boesch & Boesch-Achermann [2000]; Halperin [1979]; Lehmann & Boesch [2004]; Sugiyama [1988]; Reynolds [2005]), bonobos (86–102 min: Kuroda [1979]; White [1988, 1989]), and spider monkeys (120 min: Chapman [1988]), all which are much more fluid in their grouping patterns than species that exhibit low to moderate fission–fusion dynamics, such as hamadryas baboons (e.g., one-male units coalesce just once in 24 hr to sleep [e.g., Swedell & Plummer, 2012]), or snub-nosed monkeys (e.g., groups fission during periods of resource scarcity for periods lasting six or more days [e.g., Ren et al., 2012]).

While these aspects of ruffed lemur fission–fusion resemble patterns found in haplorrhines, ruffed lemurs also differ quite dramatically in several important respects, particularly in their patterns of subgrouping and social association. For example, despite their overall similarity in community size, both absolute (mean = 2.5 individuals) and relative (10.6%) subgroup sizes at Mangevo were small compared to all other well-studied species, including chimpanzees (range: 4–10 individuals; relative subgroup size mean = 16%), bonobos (4–22 individuals; relative subgroup size mean = 42.9%), and spider monkeys (range: 3–8 individuals; relative subgroup size mean = 14.3%), with the exception of muriquis (range: 2–5 individuals; relative subgroup size mean = 9.9%) (Table VII). Moreover, ruffed lemurs spent more time alone than did any other gregarious primate taxon reported (Table VIII). Whereas most well-studied fission–fusion species typically spend anywhere from 4.2% to 28% of their time alone, ruffed lemurs at Mangevo were without social partners nearly half of the time they were observed (48%), a pattern also described in the Nosy Mangabe community [Morland, 1991a]. The striking amount of time individuals spent solitary led Morland [1991a] to liken ruffed lemur social organization to a combination of the dispersed social systems of the nocturnal cheirogaleids [e.g., reviewed in Müller & Thalmann, 2000] and the fluid fission–fusion groupings of chimpanzees and spider monkeys. Vasey [2006] further refined this assessment by documenting the ranging and spatial association patterns of male and female red ruffed lemurs on Masoala. She found that males resembled non-gregarious nocturnal strepsirrhines in some respects (e.g., minimal overlap between male ranges) whereas females differed substantially from them in that their individual home ranges were larger than those of males and overlapped with those of multiple other females and males within their community. It is somewhat surprising that ruffed lemurs spend such a significant proportion of their time alone, as fission–fusion has long been argued to evolve when the threat of predation is lifted, either by large body size or low density predator communities [Dunbar, 1988; Kummer, 1971; Symington, 1988a; Terborgh & Janson, 1986; Wrangham, 1980]. While they are the largest extant lemurid [Fleagle, 2013], ruffed lemurs are not particularly large [Baden et al., 2008] and the predator community at Ranomafana is not only intact, but diverse [Karpanty & Wright, 2007]. Therefore, the selective pressures leading to this particular social strategy are seemingly incongruent with the hypothesis that fission–fusion results only in the perceived absence of predation threat. Recent work, however, has shown that average predation rates by fossa—among ruffed lemurs' top predators—are low, albeit temporally variable (i.e., predation events are clumped in time) [Irwin et al., 2009]. Thus, it is possible that, while predation can significantly impact ruffed lemur populations [e.g.,

TABLE VII. Cross-Taxonomic Comparisons of Community Size, and Absolute and Relative Subgroup Size

Study site	Community size	Subgroup size		N units	Method	Reference
		Absolute ($\bar{x}$ + SD)	Relative (%)			
Chimpanzees						
Bossou, Guinea	20	4.00 ± 2.41	20.0	426 days	1st observation/day	Sakura [1994]
Bossou, Guinea	19–21	5.84 ± 2.92	29.2	130 days	1st observation/day	Sugiyama [1981]
Budongo Forest, Uganda	46	6.27 ± 4.42[a]	13.6	1,824 subgroups	Maximum subgroup size before fission	Newton-Fisher et al. [2000]
Budongo Forest, Uganda	46	5.70 ± 3.48	12.4	3,164 scans	15 min scans	Newton-Fisher et al. [2000]
Budongo Forest, Uganda	59	5.01 ± 3.57[a]	10.9	5,214 scans	30 min scans	Newton-Fisher et al. [2000]
Budongo Forest, Uganda	59	7.01 ± 4.99	11.9	854 days	Cumulative subgroup size/ day (feeding subgroup)	Reynolds [2005]
Budongo Forest, Uganda	35	5.01 ± 3.57	8.5	5,214 scans	30 min scans	Reynolds [2005]
Fongoli, Sénégal		15.00[a]	42.9	unk.	Cumulative subgroup size/ day	Pruetz & Bertolani [2009]
Gombe N.P., Tanzania	57	5.60	9.8	498	unk.	Goodall [1986]
Goualougo Triangle Moto, DRC	–	4.85 ± 4.17[b]	–	493 days	Cumulative subgroup size/ day	Morgan [2007]
Kalinzu Forest—M group, Uganda	55	5.90	13.0	53 days	Cumulative 1 hr subgroup size/day	Mulavwa et al. [2008]
Kibale N.P., Kanyawara, Uganda	–	5.11	–	2,414 subgroups	Count/change in subgroup membership	Chapman et al. [1994, 1995]
Kibale N.P., Kanyawara, Uganda	–	5.24	–	8,190 scans	15 min scans	Chapman et al. [1994, 1995]
Kibale N.P., Kanyawara, Uganda	–	7.13	–	1,208 subgroups	Count/1hr before and after change in subgroup membership	Chapman et al. [1994, 1995]
Kibale N.P., Kanyawara, Uganda	44	5.60	13.0	1,050 scans	30 min scans	Wrangham et al. [1992, 1996]
Kibale N.P., Ngogo, Uganda	>140	10.27 ± 10.24	7.4	827 days	1st observation/day	Mitani et al. [2002a]
Kibale N.P., Ngogo, Uganda	145	6.68 ± 7.02	4.6	3,393 scans	30 min scans	Wakefield [2008, 2013]
Kahuzi–Biega N.P., DRC	22	4.43 ± 2.50[a]	20.1	73 subgroups	Count/change in subgroup membership	Basabose [2004]
Mahale Mountain N.P., Tanzania	29	6.20	21.0	218 subgroups	Count/subgroup attending feeding station	Nishida [1968, 1979]
Mahale Mountain N.P., Tanzania	–	12.70[b]	30.0	unk.	1st observation/day	Matsumoto-Oda et al. [1998]
Mahale Mountain N.P., Tanzania	33.4	15.50 ± 11.60	13.0	1,167 subgroups	Count/change in subgroup membership	Itoh & Nishida [2007]
Mahale Mountain N.P., Tanzania	33.4	4.00 ± 3.20	13.0	3,818 scans	10 min scans	Itoh & Nishida [2007]
Rubondo Island, Tanzania	–	3.29 ± 0.24	–	56 subgroups	Count/change in subgroup membership	Moscovice et al. [2007]
Rubondo Island, Tanzania	–	3.42 ± 0.29	–	138 subgroups	Count of nests/nest site	Moscovice et al. [2007]
Taï N.P., Côte d'Ivoire	70	3.45 ± 1.18	4.9	395 scans	1 hr scans	Doran [1997]
Taï N.P., Côte d'Ivoire	76	8.30[a]	11.0	2,912 subgroups	Count/change in subgroup membership	Boesch [1996]

TABLE VII. Continued

Study site	Community size	Subgroup size Absolute ($\bar{x}$ + SD)	Subgroup size Relative (%)	N units	Method	Reference
Taï N.P., Côte d'Ivoire	76	10.10[a]	13.2	527 subgroups	Count/change in subgroup membership	Boesch [1991]; Boesch & Boesch-Achermann [2000]
Bonobos						
Kalinzu Forest—M group, Uganda	17	8.70 ± 2.80	51.2	465 days	Cumulative 1 hr subgroup size/day	Mulavwa et al. [2008]
Lomako Forest, DRC	–	6.20	–	114 days	1st observation/day	White [1988]
Lomako Forest, DRC	–	5.40 ± 3.85	–	164 subgroups	Count/change in subgroup membership	White [1988]
Lomako Forest, DRC	10	4.33 ± 1.75	43.3	87 subgroups	Count/change in subgroup membership	White [1988]
Lomako Forest, DRC	22	7.15 ± 4.51	32.5	26 subgroups	Count/change in subgroup membership	White [1988]
Lomako Forest, DRC	21	9.69 ± 5.21	46.1	26 subgroups	Count/change in subgroup membership	White [1988]
Lomako Forest, DRC	–	5.40	–	135	unk.	Malenky & Stiles [1991]
Lomako Forest, DRC	–	5.40	–	164	unk.	Chapman et al. [1994]
Lomako Forest, DRC	36	5.80	22.0	248	unk.	Fruth & Hohmann, pers. comm. (In Boesch 1996)
Lomako Forest, DRC	11–14	4.85 ± 2.63	27.0	827 counts	Counts	Hohmann & Fruth [2002]
Lukuru, DRC	–	6.4 ± 4.63	–	121	unk.	Myers Thompson [2002]
Wamba, DRC	23	8.70	51.0	unk.	1 hr scans	Mulavwa et al. [2008]
Wamba, DRC	58	16.9 ± 11.60[b]	29.0	147 subgroups	Count/change in subgroup membership	Kuroda [1979]
Wamba, DRC	–	22.70	–	62 counts	Counts	Idani [1991]
Spider monkeys						
Barro Colorado Island, Panama	24	3.44	14.3	unk.	unk.	Milton [1981, 1993]
Manu N.P., Peru	38.5	3.88	10.1	unk.	3 min scans (feeding subgroup)	Symington [1988a,b]
Maracá Ecological Station, Brazil	22	3.01[b]	13.7	unk.	15 min scans (feeding subgroup)	Nunes [1998]
Punta Laguna, México	28.5	3.85	13.5	unk.	20 min scans	Ramos-Fernandez & Ayala-Orozco [2003]
Tinigua N.P., La Macarena, Colombia	17–18	6.50 ± 4.10	–	139 subgroups	Count/change in subgroup membership	Shimooka [2003]
Tinigua N.P., La Macarena, Colombia	17–18	5.00 ± 3.80	–	197 subgroups	Count/change in subgroup membership	Shimooka [2003]
Tinigua N.P., La Macarena, Colombia	17–18	3.70 ± 2.90	–	164 subgroups	Count/change in subgroup membership	Shimooka [2003]
Tinigua N.P., La Macarena, Colombia	24.5	3.50	10.6	unk.	unk.	Klein & Klein [1977]

TABLE VII. Continued

Study site	Community size	Subgroup size		N units	Method	Reference
		Absolute ($\bar{x} \pm$ SD)	Relative (%)			
Noel Kempf Mercado N.P., Bolivia	55	7.80	14.2	unk.	unk.	Wallace [1998]
Noel Kempf Mercado N.P., Bolivia	55	7.52 ± 6.29	–	–	Count/change in subgroup membership	Wallace [2008]
Santa Rosa N.P., Costa Rica	40	4.94 ± 4.18	12.4	1,018 scans	10 min scans	Chapman [1990]; Chapman et al. [1995]
Santa Rosa N.P., Costa Rica	26	7.30 ± 3.50	28.1	137 subgroups	Count/change in subgroup membership	Asensio et al. [2008, 2009]
Yasuni N.P., Ecuador	–	5.50 ± 2.50	–	5,258	unk.	Suarez [2003]
Yasuni N.P., Ecuador	–	4.90 ± 3.50	–	9,207 scans	15 min scans	Link & Di Fiore [2013]
Yasuni N.P., Ecuador	25	3.00	12.0	unk.	unk.	Pozo Rivera [2001, 2004]
Muriquis						
Parque Estadual Carlos Botelho, Brazil	54	3.74 ± 2.32[a]	6.9	2,440 subgroups	Count/change in subgroup membership	Coles et al. [2012]
Parque Estadual Carlos Botelho, Brazil	54	5.32 ± 3.27[a]	9.9	2,440 subgroups	Count/change in subgroup membership	Coles et al. [2012]
Parque Estadual Carlos Botelho, Brazil	23–31	2.60 ± 1.84[b]	–	202 subgroups	Count/change in subgroup membership (feeding, fruit)	de Moraes et al. [1998]
Parque Estadual Carlos Botelho, Brazil	23–31	1.83 ± 1.18[b]	–	142 subgroups	Count/change in subgroup membership (feeding, leaves)	de Moraes et al. [1998]
Estação Biológica de Caratinga, Brazil	23–31	4.89 ± 4.79[b]	–	63 subgroups	Count/change in subgroup membership (feeding, fruit)	de Moraes et al. [1998]
Estação Biológica de Caratinga, Brazil	23–31	2.82 ± 2.81[b]	–	61 subgroups	Count/change in subgroup membership (feeding, leaves)	de Moraes et al. [1998]
Capuchins						
Estação Biológica de Caratinga, Brazil	24–28	12.00 ± 7.78[b]	–	148 days	Mean subgroup size/15 days (from 5 min scans)	Lynch-Alfaro [2007]
Uakaris						
Lago Preto Conservation Concession, Peru	100+	43.50 ± 24.10[a]	–	759 hours	Maximum size/hour	Bowler & Bodmer [2009]
Howler monkeys						
Ometepe Biological Research Station, Nicaragua	–	6.36 ± 3.27[b]	–	422 subgroups	Count/change in subgroup membership	Bezanson et al. [2008]
Ometepe Biological Research Station, Nicaragua	–	5.50 ± 2.90[b]	–	596 subgroups	Count/change in subgroup membership	Bezanson et al. [2008]
Macaques						

TABLE VII. Continued

Study site	Community size	Subgroup size Absolute ($\bar{x}+SD$)	Subgroup size Relative (%)	N units	Method	Reference
Djurdjura Massif, Algeria	182	15.00–20.00[a]	–	unk. subgroups	Count/change in subgroup membership	Ménard et al. [1990]; Ménard [2002]
Geladas						
Simien Mountains N.P., Ethiopia	–	160.00[b]	–	unk.	1st observation/day	Snyder-Mackler et al. [2012]
Snub-nosed monkeys						
Baimaxueshan National N.R., China	331–480	199.00 ± 63.00[b]	–	24 subgroups	Count/change in subgroup membership	Ren et al. [2012]
Ruffed lemurs						
Nosy Mangabe S.R., Madagascar	11–16	2.50	–	84 days	1st observation/day	Morland [1991a]
Nosy Mangabe S.R., Madagascar	11–16	2.80 ± 0.26	–	60 subgroups	Subgroups encountered during census	Morland [1991a]
Masoala N.P., Andranobe, Madagascar	18–31	2.60 ± 0.55	–	5 subgroups	Number of 'core groups'	Vasey [2006]
Ranomafana N.P., Mangevo, Madagascar	24	2.54 ± 0.85	10.6	40,840 scans	5 min scans	This study

Note: Subgroup size includes only independent (adult and subadult) members unless otherwise noted.
[a]Studies where dependent offspring (juveniles or infants) are included in estimates of subgroup size.

four predation events in three days within the same ruffed lemur community; Baden, unpublished data], the perceived threat is infrequent enough that selection for greater group cohesion is weak.

Beyond general differences associated with subgroup type, ruffed lemurs also differ in their preferences for social associates. In both chimpanzee and spider monkey societies, males are typically thought of as being at the core of social dynamics [e.g., Gilby & Wrangham, 2008; Machanda et al., 2013; Slater et al., 2009; Symington, 1987; Wrangham & Smuts, 1980]. Male–male affiliative bonds tend to be stronger than either mixed-sex or female–female bonds [Fedigan & Baxter, 1984; Gilby & Wrangham, 2008; Machanda et al., 2013; Shimooka, 2003; Slater et al., 2009; but see Lehmann & Boesch, 2008; Williams et al., 2002]. Strong affiliative interactions between males have been said to play an important role in maintaining the cooperation needed in a context of high intergroup competition [Gilby & Wrangham, 2008; Link et al., 2009], as it potentially provides benefits to the resident males associated with defense and access to resources and mates [van Hooff & van Schaik, 1994], and in cooperatively competing with rival neighboring groups [Link, 2011]. While it is difficult to compare patterns of association strength across studies (due to incongruous methods of quantifying affiliation), it is clear that, contrary to the male-biased relationships observed in chimpanzees and spider monkeys, patterns of ruffed lemur association are predominantly female-centered [Morland, 1991a; this study (Fig. 4)], mirroring instead those patterns observed in bonobos [e.g., Hohmann & Fruth, 2002]. Following the same reasoning as described above for chimpanzees and spider monkeys, strong female bonds may help to facilitate cooperation during territory defense [Baden, unpublished data; Morland, 1991a; Vasey, 2006]. However, unlike chimpanzees and spider monkeys, which are male-philopatric (and, therefore, are more likely to be genetic relatives, but see [Vigilant et al., 2001; Di Fiore, 2009; Di Fiore et al., 2009]), the strong female-biased relationships observed in ruffed lemurs [Morland, 1991a; this study] are unlikely to be driven by kinship, as both males and females disperse [Baden, 2011; Baden et al., 2014; Razakamaharavo et al., 2010]. Therefore, it is unclear as to why female associations are stronger than those among males. One explanation may be in their communal breeding reproductive strategy. Because infants cannot cling at birth, litters are parked in nests and tree tangles until capable of independent travel, and it is during this time that evidence of communal breeding has been reported, including use of communal nests (crèches) and cooperative infant care (e.g., babysitting, allomaternal nursing) [Baden, 2011; Baden et al., 2013; Morland, 1989, 1990, 1991a; Tecot et al., 2013; Vasey, 2007]. Although infant care is not limited to

TABLE VIII. Cross-Taxonomic Comparison of Subgroup Type (% of Observations)

Site	Solitary			Male	Female	Mixed	Reference
	Overall	Male	Female				
Chimpanzees							
Assirik	19.0	–	–	2.0	18.0	58.0	Tutin et al. [1983]
Bossou, Guinea	–	–	–	–	49.0	42.0	Sakura [1994]
Budongo Forest, Uganda	–	–	–	8.7	3.1	73.7	Reynolds [2005]
Budongo Forest, Uganda (travel)	–	27.9	15.0	26.4	3.6	23.2	Sugiyama [1968]
Budongo Forest, Uganda (feed)	–	12.8	13.7	24.8	4.7	41.0	Sugiyama [1968]
Gombe N.P., Tanzania	18.0	–	–	10.0	24.0	30.0	Goodall [1968]
Kibale N.P., Kanyawara, Uganda	28.0	–	–	–	–	52.0	Chapman et al. [1995]
Kibale N.P., Kanyawara, Uganda	–	3.8	19.1	16.6	40.4	50.7	Chapman et al. [1995]
Kibale N.P., Ngogo, Uganda	–	–	–	–	19.7	55.9	[2008, 2013]
Mahale Mountain N.P., Tanzania	–	9.0	2.0	9.0	17.0	63.0	Matsumoto-Oda et al. [1998]
Mahale Mountain N.P., Tanzania	21.0	–	–	11.0	13.0	52.0	Nishida [1968]
TaiN.P.,Côte d'Ivoire	10.0	6.0	4.0	20.0	18.0	52.0	Boesch [1996]
Bonobos							
Lomako Forest, DRC	14.0	–	–	5.0	5.0	68.0	White [1988, 1992]
Lomako Forest, DRC	–	2.3	2.1	8.0	21.0	69.0	Hohmann & Fruth [2002]
Wamba,DRC	6.1	–	–	2.5	4.9	74.2	Kuroda [1979]
Spider monkeys							
Santa Rosa N.P., Costa Rica	–	8.0	24.0	3.0	47.0	17.0	Chapman [1990]
Capuchins							
Estação Biológica de Caratinga, Brazil	–	2.7	3.4	6.8	1.4	85.8	Lynch-Alfaro [2007]
Howler monkeys							
Ometepe Biological Research Station, Nicaragua	4.2	–	–	0.0	0.0	95.8	Bezansonet al. [2008]
Muriquis							
Parque Estadual Carlos Botelho, Brazil	–	2.0	5.0	13.4	1.2	39.4	Coles et al. [2012]
Ruffed lemurs							
Nosy Mangabe S.R., Madagascar	46.0	16.2	18.2	5.4	7.4	52.7	Morland [1991a]
Ranomafana N.P., Mangevo, Madagascar	46.0	20.7	23.5	6.8	4.7	44.4	This study

Every attempt was to made to standardize definitions of subgroup types across studies. However, some studies used subgroup types that were not obviously equivalent to our own (e.g., "adult subgroup") and were, thus, excluded here. In these cases, rows will not sum to 100%.
Solitary female category includes mothers with dependent young.

mothers [Baden et al., 2013; Morland, 1990; Vasey, 2007], there is a strong bias toward reproductive females [Baden, unpublished data], and thus maintaining strong social relationships year-round may facilitate cooperative care during the time of year when infants are dependent.

Ruffed lemurs are notable among fission–fusion taxa in that their fluid grouping patterns display both daily and seasonal components. Indeed, not only do ruffed lemur subgroups vary in size, composition, and cohesion throughout the course of a day—patterns that we have demonstrated largely resemble those of haplorrhine taxa (Tables VII and VIII)—our multivariate analyses also revealed significant, combined effects of climate, fruit availability, and female reproductive state on ruffed lemur fission–fusion dynamics. For example, we found that ruffed lemur subgroups were larger and more cohesive during the warm-wet season (Feb-May), a time that largely coincides with high fruit availability (Fig. 1). As resources became increasingly scarce—moving into the cool-wet months of June, July, and August—subgroups in our study became smaller and less cohesive. Subgroups were also smaller at lower temperatures and during periods of reduced rainfall, variables that have been closely linked with reductions in plant productivity [Dewar & Richard, 2007; Hemingway, 1996, 1998; Meyers & Wright, 1993; Overdorff, 1993]. These results are consistent with those of Morland [1991a,b], who described ruffed lemurs as having fewer inter-individual associations and spending more time alone during cool periods of resource scarcity, and with Vasey [2006], who documented the dispersion of core groups into separate core areas during both gestation and the food-scarce, cold rainy season. Together, these observations support the hypothesis that fission–fusion dynamics primarily function to reduce feeding competition in the face of fruit scarcity [Anderson et al., 2002; Chapman et al., 1995; Lehmann et al., 2007; Shimooka, 2003].

Ruffed lemur fission-fusion dynamics also varied with reproductive season. In particular, subgroups were smallest and most cohesive during the months associated with lactation and high infant dependence (October-December). This pattern was, in large part, probably driven by the initial six weeks post-partum, which comprised the period of natal nest use and exclusive maternal care [Baden, 2011; Baden et al., 2013]. Similarly, Morland [1991a] and Vasey [2006] have both noted that reproductive state influenced female gregariousness, with females in early lactation being more solitary than non-lactating females in the same months. While these patterns are not unlike observations in chimpanzees, whereby reproductive state determines much of a female's sociality [Goodall, 1986; Mitani et al., 2002b; Wakefield, 2013], they differ in that patterns of ruffed lemur fission-fusion take on both a daily and

seasonal form. Like most strepsirrhines, ruffed lemurs stand apart from chimpanzees and all other haplorrhines in their patterns of strict seasonal breeding and reproductive synchrony [Baden et al., 2013; Bogart et al., 1977a,b; Boskoff, 1977a; Rasmussen, 1985; Morland, 1993]. All females within a community generally come into vaginal estrus once during a brief, synchronized 24-72 hour period each year (i.e., the "reproductive season") [Foerg, 1982; Baden, unpublished data]. During all other times of year, female genitalia are imperforate [Foerg, 1982]. Because reproduction in this taxon is so tightly synchronized among individuals, it therefore results in a corresponding behavioral synchrony across seasons (e.g., reduced fission-fusion dynamics during early lactation). These patterns support claims that ruffed lemur social organization appears to be largely driven by the unique life history of this genus [Vasey, 2003, 2007]. We should note that the relationships described herein for the Mangevo population are derived from the first three months of lactation only. A highly gregarious period during the latter half of lactation has been described elsewhere [Vasey, 2007].

To our knowledge, these seasonal patterns of fission–fusion dynamics are unique to ruffed lemurs and appear to be consistent across sites and study periods (despite spanning several decades). It is worth noting that the few studies where ruffed lemur social dynamics do not conform to these patterns have been either very short in duration (e.g., two months during Madagascar's austral winter when subgroups are smaller and more cohesive: White [1991]), or of populations that have faced recent ecological hardships (e.g., Cyclone Gretelle significantly impacted forest structure and fruit availability: Ratsimbazafy [2002]; long-term selective logging removed large fruiting trees and affected average tree height, diameter, and density: Balko [1998]; Balko and Underwood [2005]). Thus, despite their obligate frugivory and sensitivity to habitat disturbances, ruffed lemur social flexibility has likely allowed them to persist under suboptimal ecological conditions, at least in the short term.

While the most common assumption is that fission–fusion parameters strongly depend on ecological variables and reproductive strategies of the species, demographic variables (e.g., population density, community size, number of males) can also affect subgrouping patterns [Boesch, 1996; Lehmann & Boesch, 2004]. For example, several studies have found an inverse relationship between community size and relative party size; at smaller community size, sexes showed greater cohesiveness and reduced fluidity (lower transition rates) [Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004; Sugiyama & Koman, 1979]. At present, the data available from ruffed lemurs appear to also fit this pattern (Table IX). At sites where ruffed lemur

TABLE IX. Comparison of Ruffed Lemur Community Size, Sex Ratio, and Absolute and Relative Subgroup Sizes Across Sites and Long-Term Studies

Species	Study site	Population density/km²	Social organization	Community size	Sex ratio	Subgroup size Absolute ($\bar{x} \pm$ SD)	Subgroup size Relative (%)	Study duration (months)	Sampling duration (hours)	Reference
Varecia rubra	Ambatonakolahy (Masoala N.P.)	21.5–23.3	Fission–fusion	5.5 (n = 2)	1.50	unk.	unk.	11	704	Rigamonti [1993]
Varecia rubra	Andranobe (Masoala N.P.)[a]	31.2–53.4	Fission–fusion	13.0 (n = 1)	0.38	2.60 ± 0.55	23.64	12	672	Vasey [1997, 2006]
Varecia variegata	Nosy Mangabe	29.0–43.0	Fission–fusion	11.0 (n = 2)	1.02	2.80 ± 0.26	21.54	13	1,793	Morland [1991a,b]
Varecia variegata	Vatoharanana (Ranomafana N.P.)	1.5	Dispersed monogamy	2.0 (n = 1)	1.00	2.00	100	2	112	White [1989, 1991]
Varecia variegata	Vatoharanana (Ranomafana N.P.)	3.0–6.0	Cohesive mm:mf	5.7 (n = 3)	1.44	5.67 ± 1.15	100	18	1,700	Balko [1998]
Varecia variegata	Mangevo (Ranomafana N.P.)	23.4	Fission–fusion	24.0 (n = 1)	1.38	2.54 ± 0.85	10.59	16	4,044	Baden [2011], this study
Varecia variegata	Manombo	0.25	Dispersed mm:mf	2.4 (n = 2)	0.83	2.42 ± 0.59	100	18	1,431	Ratsimbazafy [2002]

Community and subgroup sizes include adults and subadults only (infants excluded). For studies where fission–fusion was absent, community size is equivalent to subgroup size.
Sex ratios are presented as the number of adult males to every one adult female.
[a]Absolute and relative subgroup sizes based on core group sizes.

population densities were low (0.25–6 ind./km²), animals reportedly associated in small, stable pair-bonded or multimale-multifemale groups (but see discussion above regarding limitations to these studies). By contrast, animals living at higher population densities (>20 ind./km²) tended to associate in larger, more fluid multimale-multifemale groups that were characterized by both daily and seasonal patterns of fission–fusion social dynamics. These latter communities were all similar in size and sex ratio, and subgroup dynamics (e.g., average absolute and relative subgroup sizes) were remarkably similar. Unfortunately, further comparisons were not possible because comparable data were not available from all sites. In the future, it will be informative to compare the fission–fusion dynamics (e.g., transition rates, patterns of group size, and cohesion) in ruffed lemurs at sites with different population densities and among communities differing in size.

In summary, we found that black-and-white ruffed lemurs display a distinct pattern of fission–fusion dynamics that is both markedly different from and strikingly similar to haplorrhine taxa with fluid fission–fusion societies. Compared to haplorrhines, ruffed lemurs exhibited smaller subgroups, dramatically lower rates of association, and a female-centered social organization. What is more, group dynamics varied seasonally with changes in climate, fruit availability, and reproductive state. These seasonal patterns of ruffed lemur fission–fusion paired with aspects of their spatial ecology (e.g., shorter travel distances, smaller ranges, and fewer associations during the austral winter: [Baden & Gerber, in prep; Vasey, 2006]) and unique life histories (e.g., litters, seasonal breeding, and boom-bust reproduction: [Baden et al., 2013; Vasey, 2007]) are consistent with Wright's [1999] energy frugality hypothesis, which postulates that lemur traits are adaptations to conserve energy and/or to maximize use of scarce resources. However, while fission–fusion dynamics may comprise one strategy among a suite of characteristics making ruffed lemurs uniquely adapted to their harsh and unpredictable island environment, similarities between ruffed lemurs and other fluid fission–fusion species suggest that the factors shaping these patterns can select for remarkably similar behavioral strategies, particularly in convergent settings.

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