Original Research Article

Sex-Segregated Range Use by Black-and-White Ruffed Lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar

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Abstract
Ranging behavior is one important strategy by which nonhuman primates obtain access to resources critical to their biological maintenance and reproductive success. As most primates live in permanent social groups, their members must balance the benefits of group living with the costs of intragroup competition for resources. However, some taxa live in more spatiotemporally flexible social groups, whose members modify patterns of association and range use as a method to mitigate these costs. Here, we describe the range use of one such taxon, the black-and-white ruffed lemur (*Varecia variegata*), at an undisturbed primary rain forest site in Ranomafana National Park, Madagascar, and characterize sex differences in annual home range area, overlap, and daily distances traveled. Moreover, we characterize seasonal variability in range use and ask whether ranging behaviors can be explained by either climatic or reproductive seasonality. We found that females used significantly larger home ranges than males, though sexes shared equal and moderate levels of home range overlap. Overall, range use did not vary across seasons, although within sexes, male range use varied significantly with climate. Moreover, daily path length was best predicted by day length, female reproductive state, and sex, but was unrelated to climate variables. While the patterns of range use and spatial association presented here share some similarities with "bisexually bonded" community models described for chimpanzees, we argue that ruffed lemurs

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best conform to a "nuclear neighborhood" community model wherein nuclear (core) groups share the highest levels of home range overlap, and where these groups cluster spatially into adjacent "neighborhoods" within the larger, communally defended territory.

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Introduction

In many primates, individuals live, travel, and forage together in cohesive units or "social groups." Despite exhibiting variable preferences for social partners [Cords, 2002; Silk et al., 2006a, b; Schülke et al., 2010; Perry, 2013; Seyfarth et al., 2014], resource utilization [Boinski, 1988; Fragaszy and Boinski, 1995; King et al., 2009], and/or spatial position within the group [Janson, 1990a, b; Ron et al., 1996; Hall and Fedigan, 1997; reviewed in Hirsch, 2007], patterns of individual movement in these taxa are generally broadly coordinated, and range use – including home range size, overlap, and daily path length (DPL) – is more or less coincident amongst group members [Strandburg-Peshkin et al., 2015]. As such, there is expected to be little variation in individual ranging patterns among age-sex classes within cohesive social groups (though these patterns break down around natal dispersal and secondary transfer events) [Jack and Isbell, 2009, and references therein]. By contrast, in some taxa, group members are able to individually optimize the costs and benefits of group living, and groups are much less spatiotemporally constrained. In these taxa, members of socially and geographically circumscribed groups (or "communities") associate in temporary, flexible subunits (i.e., "parties" or "subgroups") that vary in size, cohesion, membership, and duration via a strategy known as "fission-fusion" [sensu Kummer, 1971; reviewed in Aureli et al., 2008]. Such behavioral flexibility allows group members to individually adjust their patterns of association in accordance with ecological and social constraints [Symington, 1990; Chapman et al., 1995; Williams et al., 2002; Mitani et al., 2002, and references therein; Lehmann and Boesch, 2004], variation which is in turn reflected in their corresponding patterns of range use [reviewed in He et al., 2019].

In chimpanzees and spider monkeys – the best-studied of the nonhuman primates exhibiting high fission-fusion dynamics – patterns of social association and range use are generally sex-segregated [Goodall, 1986; Symington, 1990; Hasegawa, 1990; Chapman and Wrangham, 1993; Williams et al., 2002]. Males tend to be more gregarious than females [Wrangham, 2000; Otali and Gilchrist, 2006; Lehmann and Boesch, 2008] and exhibit stronger social bonds with each other than either mixed-sex or female-female dyads [Fedigan and Baxter, 1984; Shimooka, 2003; Gilby and Wrangham, 2008; Slater et al., 2009; Machanda et al., 2013]. By contrast, females – particularly those with infants or dependent offspring – are more often found alone or in small same-sex parties [Nishida, 1968; Wrangham and Smuts, 1980; Goodall, 1986; Symington, 1988a, 1990; Chapman, 1990; Wrangham, 2000; Lehmann and Boesch, 2008].

Because individual movement in these taxa is generally less constrained, sex biases in social association are typically reflected in sex-segregated patterns of range use [Wrangham and Smuts, 1980; Stumpf, 2007]. Males tend to travel longer daily distances [Wrangham and Smuts, 1980; Doran, 1997; Wallace, 2008], use larger overall
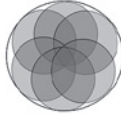
Fig. 1. Though traditionally used to characterize chimpanzees, community models of fission-fusion dynamics allow for clear predictions regarding home range (HR) size, overlap, and the spatial distribution of males and females in any nonhuman primate. White circles indicate female ranges; gray circles indicate male ranges.

home ranges [Wrangham and Smuts, 1980; Symington, 1988b, 1990; Wrangham et al., 1992; Chapman and Wrangham, 1993; Nunes, 1995; Williams et al., 2002; Shimooka, 2005], and spend more time in the peripheries of their territory than do females [Chapman, 1990; Chapman and Wrangham, 1993; Lehmann and Boesch, 2005; Mitani and Watts, 2005; Shimooka, 2005; Wallace, 2008]. Males also tend to share larger, more overlapping home ranges with other males and most, if not all, females within their community [Wrangham, 1979; Symington, 1988b; Chapman and Wrangham, 1993; Nunes, 1995; Shimooka, 2005]. Females in these same communities do not typically utilize their entire range and instead restrict their movement to smaller, more central areas within the territory [Wrangham and Smuts, 1980; Chapman and Wrangham, 1993; Williams et al., 2002; Shimooka, 2005]. Together, these patterns have been characterized by some as following a "male-bonded" community model [Lehmann and Boesch, 2005] (Fig. 1).

There is, however, notable inter- and intrapopulation variation in the patterns of association and range use observed in these species. For instance, some populations of chimpanzees (e.g., Bossou and Taï in West Africa) and spider monkeys (e.g., Yasuni) can be characterized as more closely adhering to a "bisexually bonded" community model, wherein males and females are equally gregarious, spending more time in mixed-sex parties [Boesch, 1991] and exhibiting more similar patterns of range use and overlap [Sugiyama, 1988; Sakura, 1994; Boesch, 1996; Lehmann and Boesch, 2005, 2008; Spehar et al., 2010] (Fig. 1), patterns that have been attributed to higher resource availability, lower population size/density, and reduced predation

and/or anthropogenic pressure relative to eastern sites [reviewed in Lehmann and Boesch, 2005].

This variation is further influenced by inter- and intra-annual seasonality in both resource availability and female reproduction. In fact, many argue that fission-fusion dynamics may have primarily evolved in response to shifting resource availability, allowing individuals to maximize the benefits of group living (e.g., predator avoidance, resource defense) while minimizing within-group resource competition [Boesch and Boesch-Achermann, 2000]. For instance, there is evidence that individuals from both "male-bonded" and "bisexually bonded" chimpanzee and spider monkey communities will form smaller, more dispersed foraging parties when fruit is scarce [Klein and Klein, 1977; Symington, 1988a; Mitani et al., 2002; Aureli and Schaffner, 2008; Riedel et al., 2011], when fruit is dispersed [Chapman et al., 1995; Newton-Fisher et al., 2000; Basabose, 2004; Wittiger and Boesch, 2013], or when food patches are small [Isabirye-Basuta, 1988; White and Wrangham, 1988; Chapman, 1990; Potts et al., 2011; Wittiger and Boesch, 2013]. These seasonal changes in fission-fusion dynamics are often reflected in seasonal patterns of range use, including shorter daily travel distances [Doran, 1997; Herbinger et al., 2001; Matsumoto-Oda, 2002; Moore et al., 2018] and/or smaller, less overlapping home ranges during fruit lean periods [Nakamura et al. 2013; Moore et al. 2018]. Relationships between food availability, subgroup size, and range use do, however, vary. For instance, some communities range in smaller subgroups or utilize smaller home ranges [Herbinger et al., 2001] during periods of resource abundance, whereas others exhibit little to no correspondence between resource availability and either fission-fusion dynamics [Hashimoto et al., 2003; Wakefield, 2008] or ranging behaviors [Boesch and Boesch-Achermann, 2000; Basabose, 2005].

While the vast majority of primate fission-fusion literature has traditionally focused on chimpanzees and spider monkeys, there is growing evidence that fission-fusion dynamics are, in fact, more common than previously recognized [Aureli et al., 2008], and that the demographic, ecological, and social variables described above can be applied more broadly to explain fission-fusion dynamics across the primate order. For instance, in many nonhuman primates, group fissions and concomitant changes in ranging behavior commonly occur within a feeding context [Izar et al., 2012; Ren et al., 2012; Dolado et al., 2016, 2017] and/or in accordance with social variables such as subgroup size or the presence of sexually receptive mates [Dias and Strier, 2003; Bezanson et al., 2008; Strier, 2018; Ellis and Di Fiore, 2019]. Here, we add to this growing body of literature by quantifying patterns of range use and overlap in a strepsirrhine with high fission-fusion dynamics, the black-and-white ruffed lemur (*Varecia variegata*) [Baden et al., 2016].

Ruffed lemurs are relatively large-bodied (2.5–4.8 kg [Baden et al., 2008]), arboreal frugivores endemic to the eastern rain forests of Madagascar [Morland, 1991a; Rigamonti, 1993; Balko, 1998; Vasey, 2000; Ratsimbazafy, 2002; Baden, 2011]. Ruffed lemurs live in large social groups (e.g., 11–31 individuals) that are characterized by high levels of fission-fusion social dynamics [Morland, 1991a, b; Rigamonti, 1993; Vasey, 1997; Baden, 2011; Baden et al., 2016; Holmes et al., 2016]. Aspects of their behavior, including activity budgets, foraging patterns, and subgroup size, composition, and cohesion vary by season, resource availability, and female reproductive state [Morland, 1991a, b; Rigamonti, 1993; Vasey, 2002, 2005, 2006; Baden et al., 2016; Beeby and Baden, in review]. For black-and-white ruffed lemurs, in particular, ani-

mals in primary rain forest habitats tend to spend more time solitary and are found in smaller, more cohesive subgroups during times of resource scarcity, a period that aligns with early lactation during austral winter months [Morland 1991a; Baden et al., 2016; but see Holmes et al., 2016 for patterns in disturbed sites]. Moreover, recent work has found that ruffed lemurs reduce travel time, increase resting time, and exhibit greater use of higher canopy levels during this same period, a "time minimizing" behavioral strategy that is thought to reduce nutritional requirements for maintaining energetic homeostasis during periods of low fruit availability [Beeby and Baden, in review]. As temperature and rainfall increase, so too does fruit availability, ruffed lemur activity, and the emergence of larger, less cohesive mixed-sex subgroups [Baden et al., 2016; Beeby and Baden, in review].

While there has been a recent uptick in studies investigating seasonality in ruffed lemur behavioral ecology and fission-fusion dynamics [Holmes et al., 2016; Baden et al., 2016; Baden et al., 2020; Beeby and Baden, in review], those characterizing seasonality in ruffed lemur range use remain limited and provide incongruous results. For instance, one study of red ruffed lemurs (*Varecia rubra*) from the Masoala Peninsula described females as utilizing large, seasonally variable home ranges that overlapped extensively with those of other females, and which encompassed the smaller, nonoverlapping territories of males [Vasey, 2006]. Like eastern chimpanzees, ranging behaviors were sex-segregated, though patterns described by Vasey [2006] might be best characterized as "female bonded" (Fig. 1). Nevertheless, like many primates with fission-fusion dynamics, patterns of red ruffed lemur range use were not uniform throughout the year; home range area, overlap, and daily distances traveled shifted in accordance with resource availability and female reproductive state. During warm, wet resource abundant months, females used large home ranges that overlapped extensively with other females in the community. Female ranging behaviors were significantly reduced – home ranges became smaller and nonoverlapping – during periods of resource scarcity (cool, dry and cool, wet months), seasons that coincided with mating, gestation, and high infant dependence. Male range use did not vary by season or female reproductive state, suggesting that differences in range use were driven almost entirely by females [Vasey, 2006]. Moreover, daily distances traveled did not vary between sexes, except within the context of the premating period, when males traveled significantly farther than females in search of mates. As in an earlier study [Rigamonti, 1993], animals were observed traveling longer daily distances in warmer months, and both male and female travel was significantly related to female reproductive state: travel was most constrained during the gestation period, followed by nonreproductive seasons, and least constrained when females were lactating [Vasey, 2006]. By contrast, Morland's [1991a] study of black-and-white ruffed lemurs (*V. variegata*) on Nosy Mangabe described males as ranging farther (i.e., using larger annual home ranges that overlapped with multiple adjacent communities) and traveling on average significantly longer daily distances than females, more akin to the patterns described of "male-bonded" chimpanzee communities (Fig. 1). However, in accordance with patterns described for red ruffed lemurs [Rigamonti, 1993; Vasey, 2006], both males and females were more active, spending more time traveling, covering greater daily distances, and utilizing larger home ranges during warm versus cool season months. While these early results stand in stark contrast, previous research has noted substantial interpopulation variability in other aspects of their demography and social behavior, including population density, social organization, and

affiliative interactions [reviewed in Baden et al., 2016], much like the regional variation noted in chimpanzees, suggesting that ruffed lemur range use may be equally as variable.

Because shared range use provides individuals the opportunity for repeated social interactions [Clutton-Brock, 1989; Kossinets and Watts, 2006], it is critical that studies consider individual patterns of range use and overlap when investigating the evolution of social behavior, particularly within taxa exhibiting high fission-fusion dynamics [e.g., Frère et al., 2010; Carter et al., 2013; Best et al., 2014; Strickland et al., 2014; Baden et al., 2020]. Thus, to broaden our understanding of ruffed lemur social behavior, including patterns of social association and fission-fusion dynamics, we must also improve our understanding of ruffed lemur range use. To this end, we characterize the annual ranging patterns, including home range area, overlap, and DPL, within a single *V. variegata* community during a 1-year period. Further, we evaluate whether and how ruffed lemur range use varies with seasonal shifts in their ecology and reproductive physiology. Based on earlier findings in this and other nonhuman primate species with high fission-fusion dynamics, we hypothesize that (H1) patterns of ruffed lemur range use will vary in accordance with climatic seasonality, as do their activity patterns, use of forest canopy strata [Beeby and Baden, in review], and fission-fusion social dynamics [Baden et al., 2016]. Given the dispersed nature of their social organization and that animals spend nearly 50% of their time alone [Baden et al., 2016], resource competition is presumed low and equitable between sexes in this population. We therefore predict that (P1.1) sexes will not differ in their patterns of range use across climatic seasons. However, Madagascar's pronounced and unpredictable climatic seasonality has created conditions that have resulted in resource constraints for lemurs more broadly, favoring adaptations that either maximize energy intake or minimize energy expenditure [Richard and Dewar, 1991; Wright, 1999; Pereira et al., 1999; Dewar and Richard, 2007]. Many lemurs minimize activity (travel less, rest more) during fruit-lean seasons, presumably as an energy conservation strategy [Tecot, 2008; Campera et al., 2014; Irwin et al., 2015; Baden and Beeby, in review]. For this reason, we predict that both males and females will (P1.2) travel less (i.e., shorter daily travel distances), and adopt home ranges that are (P1.3) smaller and (P1.4) less spatially overlapping during cool, wet periods of low resource abundance to minimize resource competition and thereby energy expenditure. By contrast, we expect animals to (P1.5) travel farther and have (P1.6) larger, (P1.7) more overlapping ranges during periods of high resource availability (e.g., warm-wet seasons), maximizing energy intake while fruits are available. Finally, because cool-dry periods align with rising resource abundance, we predict that (P1.8) home range size, (P1.9) overlap, and (P1.10) daily distances traveled will be intermediate to those exhibited during either cool-dry or warm-wet periods.

Alternatively, because patterns of resource availability are largely, though imprecisely concordant with patterns of ruffed lemur reproduction, we hypothesize that (H2) range use may instead reflect the unique mating strategies of the species [Baden, 2011; Baden et al., 2013]. In this regard, we predict that (P2.1) males and females will differ in their patterns of range use dependent on their reproductive season. We predict that males will (P2.2) travel more, and use ranges that are (P2.3) relatively larger and (P2.4) more overlapping with females during the brief mating and subsequent gestation season than during either nonbreeding or lactation seasons (i.e., mating/gestation > nonbreeding or lactation). By contrast, we predict that females will (P2.5)

Table 1. Hypotheses and predictions for seasonal patterns of ranging behaviors in black-and-white ruffed lemurs

Hypotheses and predictions		Expected pattern
H1. Patterns of ruffed lemur range use will vary in accordance with environmental seasonality		
P1.1	Sexes will not differ in their patterns of range use by climatic season	M = F
P1.2	Daily travel distances will be shortest during the cool-wet season	DPL_{Both}: WW, CD > CW
P1.3	Home ranges will be smallest during the cool-wet season	KDE_{Both}: WW, CD > CW
P1.4	Home ranges will overlap the least during the cool-wet season	$UDOI_{Both}$: WW, CD > CW
P1.5	Daily travel distances will be longest during the warm-wet season	DPL_{Both}: WW > CD, CW
P1.6	Home ranges will be largest during the warm-wet season	KDE_{Both}: WW > CD, CW
P1.7	Home ranges will overlap the most during the warm-wet season	$UDOI_{Both}$: WW > CD, CW
P1.8	Daily travel distances in the cool-dry season will be intermediate to those exhibited during either cool-dry or warm-wet periods	DPL_{Both}: WW > CD > CW
P1.9	Home ranges will be intermediate in the cool-dry season to those exhibited during either cool-dry or warm-wet periods	KDE_{Both}: WW > CD > CW
P1.10	Home ranges overlap in the cool-dry season will be intermediate to those exhibited during either cool-dry or warm-wet periods	$UDOI_{Both}$: WW > CD > CW
H2. Patterns of ruffed lemur range use will vary in accordance with reproductive seasonality		
P2.1	Sexes will differ in their patterns of range use across female reproductive season	M ≠ F
P2.2	Males will travel longer daily distances during the mating/gestation versus either nonbreeding or lactation seasons	DPL_{Male}: M/G > NB, L
P2.3	Males will use larger home ranges during mating/gestation versus either nonbreeding or lactation seasons	KDE_{Male}: M/G > NB, L
P2.4	Males will exhibit greater home range overlap during mating/gestation versus either nonbreeding or lactation seasons	$UDOI_{Male}$: M/G > NB, L
P2.5	Females will travel longer distances when energetically unconstrained by reproduction	DPL_{Female}: NB > M/G, L
P2.6	Females will utilize larger home ranges when energetically unconstrained by reproduction	KDE_{Female}: NB > M/G, L
P2.7	Females will utilize more overlapping ranges when energetically unconstrained by reproduction	$UDOI_{Female}$: NB > M/G, L
P2.8	Females will travel the shortest daily distances during lactation and high infant dependence	DPL_{Female}: NB, M/G > L
P2.9	Female home range size will be smallest during lactation and high infant dependence	KDE_{Female}: NB, M/G > L
P2.10	Female home ranges will overlap more with other females during lactation than mating/gestation to facilitate communal créching	$UDOI_{Female}$: M/G < L

DPL, daily path length; KDE, kernel density estimate, i.e., home range size; UDOI, utilization distribution overlap index, i.e., home range overlap. Environmental seasonality: WW, warm-wet; CW, cool-wet: CD, cool-dry. Reproductive seasonality: NB, nonbreeding; M/G, mating/gestation; L, lactation.

travel relatively longer distances and utilize (P2.6) larger, (P2.7) more overlapping ranges with other members of their social community (both males and females) when energetically unconstrained by reproduction (i.e., nonbreeding > gestation or lactation). We further predict that (P2.8) female home range size and (P2.9) daily distance

traveled will be most constrained (i.e., smallest and shortest) during the period of lactation and high infant dependence, but that these (P2.10) home ranges will nevertheless overlap more with other females during lactation than mating/gestation due to their communal créching infant care strategy (i.e., gestation < lactation) [Baden et al., 2013; Baden, 2019]. In other words, while we expect range size to contract during the communal breeding period, we nevertheless expect female range use to shift toward overlapping with other breeding females to facilitate shared infant care. See Table 1 for a synthesis and summary of hypotheses and predictions as they relate to seasonality.

Finally, to contextualize ruffed lemur ranging behaviors within the broader primate literature, we test the hypothesis that (H3) ruffed lemurs adhere to a "female-bonded" community model, based on details described by Vasey [2006]. If this is the case, we predict that females will use home ranges that are (P3.1) larger, and (P3.2) more overlapping (with both males and females) than males, and that males will use (P3.3) small, (P3.4) mutually exclusive ranges relative to each other.

Methods

Study Site and Subjects

Data presented here were collected from one black-and-white ruffed lemur (*V. variegata*) community at Mangevo bushcamp in Ranomafana National Park, Madagascar (RNP) during 1 year of observation (January to December 2008). Mangevo (21°22'60" S, 47°28'0" E) is a mid-elevation (660–1,200 m) primary rain forest site within the southeastern parcel of RNP, 435 km^2 of continuous montane rain forest 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]).

At the time of this study, the community included 24 adults and subadults (8 adult females, 11 adult males, 5 subadult males). Nineteen infants were born in mid-October and were present from October to December 2008. Of the adults, 5 females and 3 males were radio-collared and targeted for regular follows. Individuals with collar tags (but no radio-collar, *n* = 16) were opportunistically targeted for focal follows. Sampling efforts resulted in a total of 4,044 focal observation hours.

Data Collection
Behavioral Monitoring

Two teams of 4 observers each conducted dawn-to-dusk follows on focal individuals (i.e., 2 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. Animals were never sampled on consecutive days, and every effort was made to follow all subjects 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 animal for that observation period. Observation periods ranged in duration between 8 and 11 h 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. 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 [see Baden et al., 2016, for details]. We should note, however, that average group spread is generally small (8.02 ± 7.21 m) – rarely exceeding 20 m, except in instances of travel – and individuals spend 48% of their time alone [Baden et al. 2016]. 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].

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We collected simultaneous data on subgroup location from the approximate group center at 10-min intervals using a handheld Garmin® HCx GPS unit. Spatial coordinates were recorded only if estimated positional error was less than 10 m.

Data Analysis

We performed home range analyses with Home Range Tools [Rodgers et al., 2007] add-on for ArcGIS (ESRI, Redlands, CA, USA). We did not subsample ranging data, as this has been shown to reduce the accuracy and precision of home range estimates [De Solla et al., 1999; Blundell et al., 2001; Fortin and Dale, 2005; Fieberg, 2007]. We did, however, limit our analyses to only those spatial coordinates for which corresponding data on subgroup size and composition were available (*n* = 21,748 points). From this data set, we calculated the communal home range (i.e., the home range used by all members of the focal ruffed lemur community), as well as individual home ranges for each of its members. Individual home ranges were calculated using location points collected while an individual was the subject of focal observations, as well as when the individual was a member of the subgroup being followed (i.e., was recorded as present during a focal follow of another individual).

Certain individuals were difficult to locate and were peripheral to social interactions within the community. Because home range analyses should use data that encompass the full range of movement behavior exhibited by an animal [Harris et al., 1990], data from infrequently encountered animals may not be representative of their true movement behaviors. We therefore investigated the relationship between sample size and measures of both annual and seasonal home range area with an incremental area analysis (i.e., increment plots) [Kenward and Hodder, 1996; Kenward, 2001], whereby we iteratively added spatial locations and estimated home range size for each individual to evaluate asymptotic stability in our estimates. This was done for the communal territory, as well as for individual territories within the larger communal range. We found that communal territory stabilized after ~500 fixes. Annual individual home range estimates tended to asymptote earlier, after approximately 250 location points. To account for monthly variation in sampling effort, we omitted animals with fewer than 250 location points spread across 25 sampling days throughout the year from annual home range analyses. It is important to note that, in a majority of cases, sampling effort was evenly distributed throughout the year. Thus, while 250 location points was a minimum criterion for infrequently encountered animals, most individuals included in the analysis were sampled at least twice as often. Similarly, estimates of seasonal home range area reached asymptotes around 100 location points, and thus to ensure representative sampling, individuals with fewer than 100 location points spread across 10 sampling days within a given season were omitted from further analyses. See Appendix I for details.

Annual Range Use and Overlap

Using the data sets described above, we estimated range use in two ways: using kernel density estimates (KDEs) and minimum convex polygons (MCPs). The first method, KDEs, are widely regarded as a robust probabilistic estimator for making inferences about home range size, as well as about patterns of use within the home range (utilization distribution [Worton, 1989; Powell, 2000]). KDEs were calculated using a bivariate normal distribution, rescaling X-Y coordinates to unit variances as recommended by Silverman [1986]. Raster cell size was set to 10 × 10 m to accommodate most GPS errors, while maintaining a fine enough resolution for estimating accurate home range overlap indices. However, some of the larger GPS errors (10 m) may cause some spatial points to be placed in an adjacent cell to the correct one, but this would occur rarely and randomly to not cause systematic bias. Kernel home range estimators are sensitive to the choice of smoothing parameter [Silverman, 1986]; this is especially true with large data sets and when animals exhibit strong site fidelity [Hemson et al., 2005]. Given our large data set and observations that animals regularly traverse the same areas, we used the root-n smoothing parameter, as it has been found to overcome these issues [Steury et al., 2010]. Home range size was estimated for the community as a whole, as well as for all individuals separately, and ranges were evaluated using 95% kernel isopleths.

The second method, MCPs, creates individual polygons that include all locations where a particular individual was recorded [Mohr, 1947]. However, the method suffers from sample size

effects and is greatly affected by outliers, such that MCP estimates often contain large areas never used by an animal [Powell, 2000; Laver and Kelly, 2008]. MCP estimates might also affect small-scale comparisons, i.e., within species or populations, although when large differences occur most of the variation is due to real differences [Nilsen et al., 2008]. This method was used exclusively to facilitate comparison with previous studies of ruffed lemurs. To help mitigate outlier effects, we calculated 95% MCPs via the fixed mean, a method employed to control for rare but observed excursions outside of the home range.

In addition to home range area, we also generated estimates of home range overlap. Kernel overlap was calculated using a utilization distribution overlap index (UDOI [Fieberg and Kochanny, 2005]) implemented in the R package adehabitat [Calenge, 2006]. The UDOI is an index of space use sharing between two utilization distributions. If home ranges are uniformly distributed, UDOI values can range from 0 to 1, with a UDOI of 0 indicating no home range overlap and a UDOI of 1 indicating 100% overlap. Values can also be >1 if both UDs are nonuniformly distributed and also have a high degree of overlap. Values <1 indicate less overlap relative to uniform space, whereas values >1 indicate higher than normal overlap relative to uniform space. We calculated annual and seasonal UDOIs for all pairs of individuals included in our study. MCP overlap in individual home ranges was calculated as the proportion of shared area between two polygons. MCP overlap was calculated for communal home range area and individual annual home range areas only.

Neighborhood Analysis

To contextualize annual patterns of ruffed lemur range use and overlap within the broader primate fission-fusion literature, and test the hypothesis that (H3) ruffed lemurs adhere to a "female-bonded" community model, we ran a hierarchical cluster analysis using methods modeled after Williams et al. [2002]. We used the Mean Center tool in the Spatial Statistics Toolbox of ArcGIS Pro 2.5 to identify geographic centers (i.e., center of concentration) of each individual's 95% KDE home range. From this, we used the *dist* function in the r package factoextra [Kassambara and Mundt, 2018] to create a dissimilarity matrix by summing the squared Euclidean distances between the mean centers of all pairs of individuals within the community. Dissimilarity metrics were centered and scaled prior to further analysis, as recommended by Becker et al. [1988]. We then used the "average" agglomeration method of the *hclust* function in the package NbClust [Charrad et al., 2014] to produce a dendrogram, which allowed us to visualize the similarities between individual ranges [Sokal and Michener, 1958]. Based on the final dendrogram, we defined the smallest reducible clusters of individuals sharing the most similar ranging patterns as "nuclear groups" or "core groups," which further clustered into larger agglomerations of individuals, which we termed "neighborhoods" following Williams et al. [2002].

Seasonal Range Use

We consider a home range as "the space which the animal both uses and traverses" during an ecologically meaningful time period [Burt, 1943]. Thus, to further investigate patterns of ruffed lemur spatial ecology, we also calculated seasonal measures of individual home range area and overlap. Specifically, we used data on climate, phenology, and female reproductive state to separate months into discrete seasons with intervening transitional periods [see Baden, 2011, and Baden et al., 2016, for detailed methods] and then analyzed data in accordance with the *climatic* or *reproductive season* in which they were collected.

Measures of fruiting seasonality and climate were closely associated [Baden et al., 2016]. We therefore used natural breaks in the data to categorize ranging coordinates as falling into one of three *climatic seasons* (warm-wet/peak fruiting: January to February 2008; cool-wet/fruit scarcity: May to July 2008; and cool-dry/low-to-moderate fruiting: August to September 2008; March, April, and October were considered transitional seasons and were excluded from this analysis), as well as one of three *reproductive seasons* (nonbreeding: January to June 2008; gestation: July to October 2008; lactation: November to December 2008) (Appendix II; see also Fig. 1 in Baden et al. [2016]).

Table 2. Individual annual home range area and overlap

Collar ID	Sex	Located days	Location points	95% MCP, ha	95% kernel, ha
Radio-Blue	F	90	4,277	38.7	20.6
Radio-Blue-Green	F	107	4,578	32.9	19.4
Radio-Orange	F	75	3,386	26.6	18.7
Radio-Red	F	92	3,960	19.6	14.1
Radio-Blue-Yellow	F	72	3,640	13.6	11.5
Female mean		87.2	3,968.2	26.3	16.9
Black-Green	M	48	808	22.8	17.0
No collar	M	49	735	18.3	13.8
Radio-Black-Green	M	74	2,163	20.6	16.1
Radio-Purple-Silver	M	76	2,403	14.8	12.3
Black-Blue	M	58	1,792	14.9	12.0
Red-Green	M	58	1,276	15.8	12.4
Yellow-Purple	M	56	1,607	15.0	12.7
Male mean		59.9	1,540.6	17.5	13.8
p				0.04	0.03

|	Sex-sex	Number of dyads	Overlap	
			95% MCP	95% kernel
	Female-female	10	0.41±0.09	0.16±0.05
	Male-male	21	0.35±0.07	0.24±0.09
	Female-male	35	0.40±0.05	0.29±0.07
	p		0.62	0.70

MCP, minimal convex polygon.

Daily Range Use

Finally, to gain a finer-scale understanding of daily range use, we calculated DPLs for each individual as the sum of the Euclidean distances between consecutive GPS coordinates taken every 10 min. We included only full-day follows of focal individuals for which locations were recorded completely between morning and evening sleep trees, or data collection started prior to 07.00 h with ≥9 subsequent hours of observation and fewer than 5% missing observations.

Statistical Analyses

All analyses were conducted in R version 3.6.2 (R Core Team 2019). Alpha was set a priori at $\alpha = 0.05$. Individual home range area and overlap were statistically compared by sex or subgroup type and season using a combination of nonparametric Skillings-Mack and Mann-Whitney U tests. Daily path lengths were analyzed using a generalized linear mixed-effects model in the lme4 package [Bates et al., 2014] in R. Fixed effects included sex, day length, mean daily rainfall, a categorical classification of climatic season, a categorical classification of reproductive state, and the presence and number of infants. To explicitly account for individual variation in DPL, we included individual ID as a random effect. Using additive and interactive effects of our variables of interest, we a priori constructed biologically driven models; we evaluated model parsimony using Akaike's information criterion with a small sample size bias correction. To incorporate model selection uncertainty, we model-averaged all parameter estimates [Burnham and Anderson, 2002].
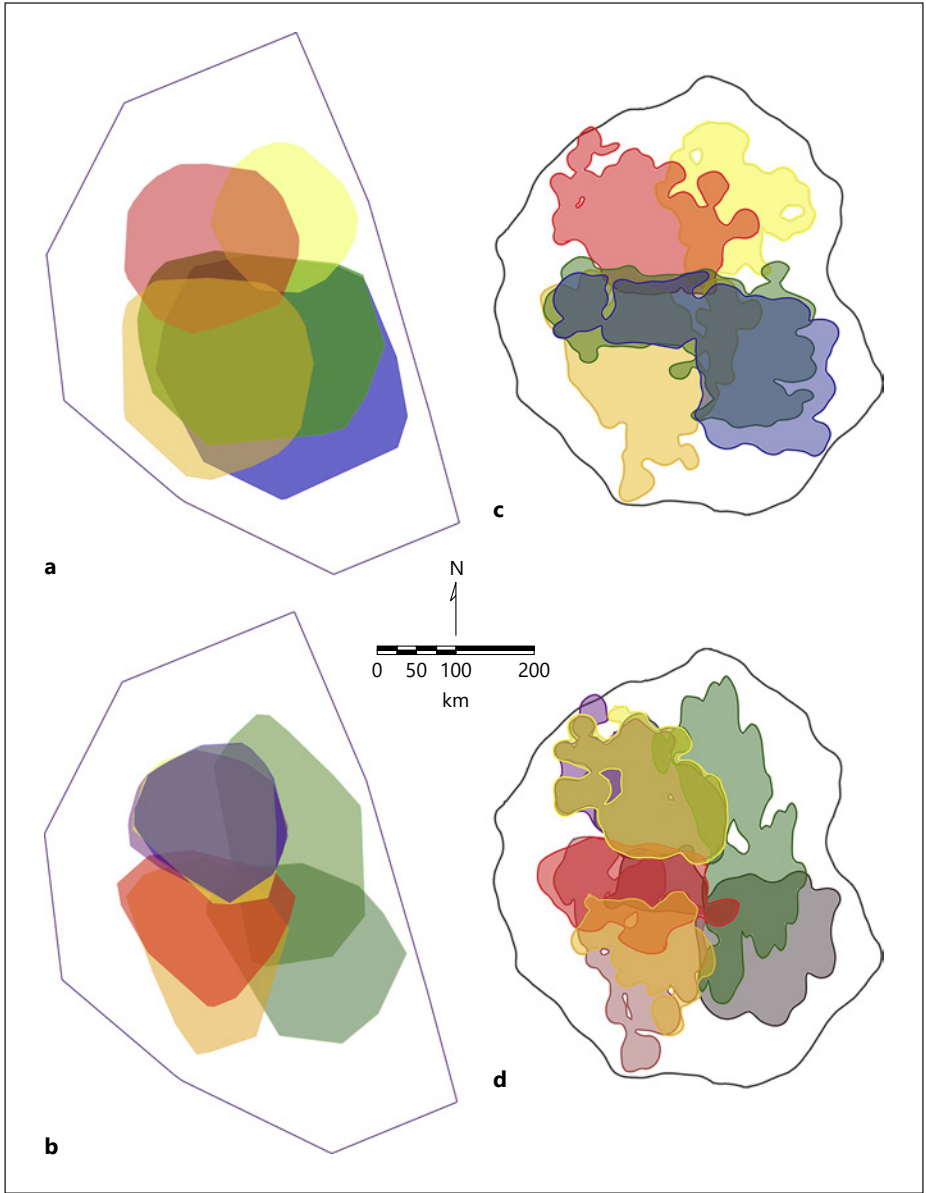
Fig. 2. Differences in annual home range size and overlap for females (**a**, **c**, top, *n* = 5) and males (**b**, **d**, bottom, *n* = 8) using minimum convex polygon (**a**, **b**, left) and 95% kernel density estimates (**c**, **d**, right).

Results

Annual Range Use

Home range estimates for the entire Mangevo ruffed lemur community were between 87 ha (KDE) and 120 ha (MCP). Within the community, individual annual home ranges varied between 11.5 and 20.6 (KDE) and 13.6 and 38.7 ha (MCP). Females ($n = 5$) used significantly larger annual home ranges than did males ($n = 7$) (MCP: Mann-Whitney U = 10.0, $p = 0.04$; kernel: Mann-Whitney U = 9.0, $p = 0.03$; Table 2). On average, female home ranges were estimated to encompass 16.9 ± 1.74 ha (KDE) to 26.3 ± 4.50 ha (MCP), whereas an average male's home range was estimated to cover 13.04 ± 0.98 ha (KDE) to 17.5 ± 1.22 ha (MCP) (Fig. 2).

Neither sex used the entire communal home range. Rather, males and females concentrated their total annual space use to only a proportion of the larger communal territory. Females used, on average, between 19.2 and 21.8% of the total community home range (KDE: mean proportion of communal range = 19.2%, $n = 5$, range = 13.1–23.5%; MCP: mean proportion of communal range = 21.8%, $n = 5$, range = 11.3–32.2%), while males used between 11.5 and 15.7% (KDE: mean proportion of communal range = 15.7%, $n = 7$, range = 13.7–19.4%; MCP: mean proportion of communal range = 11.5%, $n = 7$, range = 10.0–14.1%).

Across same-sex and mixed-sex dyads, home range overlap was low to moderate (KDE: 16–29%; MCP overlap: 35–41%), and sexes did not differ significantly in their proportion of home range overlap (Table 2; Fig. 2).

Neighborhoods

The hierarchical clustering analysis of pairwise dissimilarity indices identified four spatial clusters within the full-year data set that broadly corresponded to nuclear "core groups" of preferred male-female dyads (presumed mates) and mothers and their predispersal aged offspring. These clusters further sorted into two adjacent northern and southern "neighborhoods" within the larger communal range (Fig. 3).

Seasonal Range Use

Overall, individual home range size did not vary significantly across climatic seasons (Skillings-Mack test, SM = 4.87, df = 2, $p = 0.09$), although patterns of range use did differ between sexes (Table 3; Fig. 4). Within sexes, female home range size did not vary significantly by climatic seasons (Skillings-Mack test, SM = 3.60, df = 2, $p = 0.17$). By contrast, males exhibited marked seasonal variability in home range size (Skillings-Mack test, SM = 8.14, df = 2, $p = 0.02$). Males used significantly smaller home ranges during the cool-wet season than either the cool-dry season (Wilcoxon signed ranks, $Z = 28.0$, $p = 0.02$) or the warm-wet season (Wilcoxon signed ranks, $Z = 15.0$, $p = 0.04$) (Fig. 4). Male home ranges did not differ significantly between cool-dry and warm-wet seasons (Wilcoxon signed ranks, $Z = 10.0$, $p = 0.50$). Further, male and female home range sizes differed in two of three climatic seasons: males used significantly smaller home ranges than females during the cool-wet (females = 14.59 h, males = 6.42 ha; Mann-Whitney U = 3.0, $p = 0.02$) and warm-wet seasons (females = 16.38 ha, males = 9.64 ha, Mann-Whitney U = 3.0, $p = 0.05$; Table 3). Home range areas were similar in size only during the cool-dry season, when female range use decreased (females = 11.84 ha, males = 10.69 ha, Mann-Whitney
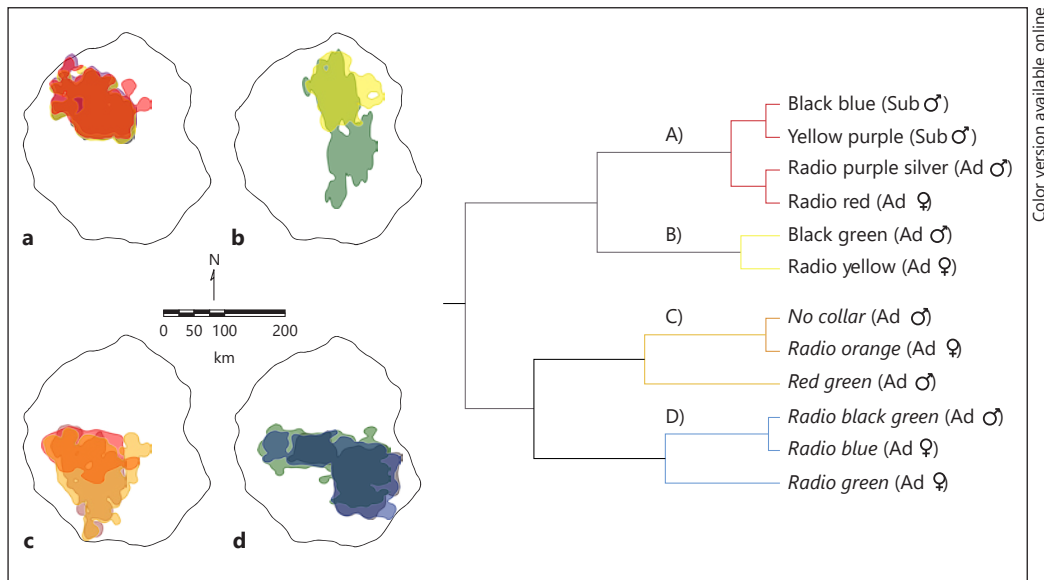
Fig. 3. Nuclear (core) groups and neighborhoods as illustrated by overlapping 95% kernel density estimates of annual home ranges (left) and the dendrogram resulting from hierarchical clustering analysis of averaged Euclidean distances between individual centers of range use (right) by members of the Mangevo ruffed lemur community. Nuclear groups are denoted by **a–d** (left and right). A, B on the dendrogram indicate membership in the northern neighborhood; C, D indicate membership in the southern neighborhood.

$U = 13.0$, $p = 0.53$; Table 3). We found no significant difference in home range overlap across seasons among same- and mixed-sex dyads (Skillings-Mack test, $SM = 2.05$, df = 2, $p = 0.36$).

By contrast, there was no discernable variation in spatial community structure for females or males across reproductive seasons (Table 3). Overall, sexes did not differ significantly in home range size (Skillings-Mack test, $SM = 1.07$, df = 2, $p = 0.59$) or overlap (Skillings-Mack test, $SM = 2.04$, df = 2, $p = 0.36$) across reproductive seasons, nor did home range size (Skillings-Mack test, $SM_{males} = 1.79$, df = 2, $p = 0.41$; $SM_{females} = 0.400$, df = 2, $p = 0.82$) or overlap (Skillings-Mack test, $SM_{MM} = 1.66$, df = 2, $p = 0.44$; $SM_{FF} = 0.95$, df = 2, $p = 0.62$; $SM_{MF} = 0.50$, df = 2, $p = 0.78$) vary significantly within sexes across reproductive seasons.

Daily Range Use

Overall, females and males did not differ in their DPLs (Mann-Whitney $U = 9,323.5$, $p = 0.926$). Females traveled, on average, a daily distance of $1,659.28 \pm 555.21$ m whereas males traveled an average of $1,673.83 \pm 598.69$ m. However, when included as a fixed effect in our mixed models, we found strong support that DPL was positively related to day length ($\hat{\beta} = 0.654$, SE = 0.111) and varied with reproductive season (model weight = 88.1%; Table 4); the only two models with any support included both of these variables (Table 4). We also found strong support for a sex dif-

Table 3. Average seasonal home range area and overlap between sexes

a Home range area (ha) by climatic season

Sex	n	Warm-wet	n	Cool-wet	n	Cool-dry	p
Females	8	15.53±5.04	5	12.79±5.82	5	11.84±2.37	ns
Males	5	8.78±3.17	7	6.08±1.09	7	10.69±2.48	*
p		*		*		ns	

b Home range overlap (UDOI) by climatic season

Overlap type	n	Warm-wet	n	Cool-wet	n	Cool-dry	p
Female-female	28	0.21±0.36	10	0.11±0.21	10	0.12±0.06	ns
Female-male	40	0.29±0.46	35	0.31±0.57	35	0.34±0.54	ns
Male-male	10	0.09±0.27	21	0.30±0.56	21	0.35±0.75	ns
p		ns		ns		ns	

c Home range area (ha) by reproductive season

Sex	n	Nonbreeding	n	Gestation	n	Lactation	p
Females	5	14.76±5.45	5	12.12±2.30	7	11.40±2.78	ns
Males	7	9.93±2.55	8	9.24±2.50	5	8.64±2.07	ns
p		ns		ns		ns	

d Home range overlap (UDOI) by reproductive season

Overlap type	n	Nonbreeding	n	Gestation	n	Lactation	p
Female-female	10	0.15±0.30	10	0.12±0.21	15	0.14±0.32	ns
Female-male	35	0.22±0.39	40	0.33±0.56	30	0.33±0.62	ns
Male-male	21	0.16±0.36	28	0.33±0.77	10	0.07±0.18	ns
p		ns		ns		ns	

UDOI, utilization distribution overlap index. Comparisons include only those individuals with ≥10 sampling days per season and home range estimates from at least 2 of 3 seasons. Note that statistical comparisons were among only those individuals for which data were available from at least 2 of the 3 sampling periods. * $p < 0.05$.

ference by reproductive season and day length; the model including the sex variable had 7 times the support as the model without it (0.881 vs. 0.119). We found males to generally move more per day than females ($\hat{\beta} = 11.49$, SE = 3.79; males = 1, females = 0), with the strongest difference occurring in the lactation season (Table 4). Standardizing to 12 h of daylight, DPL in both the nonbreeding season (female: 1,761 ± SE 57.6 m; male: 1,948.6 ± SE 122.0 m) and gestation seasons (female: 1,736.1 ± 99.48 m; male: 1,917.0 ± 296.8 m) were more similar than during lactation, when daily distances traveled by females (840.6 ± SE 106.2 m) were far more restricted than males (1,824.6 ± SE 196.7 m).
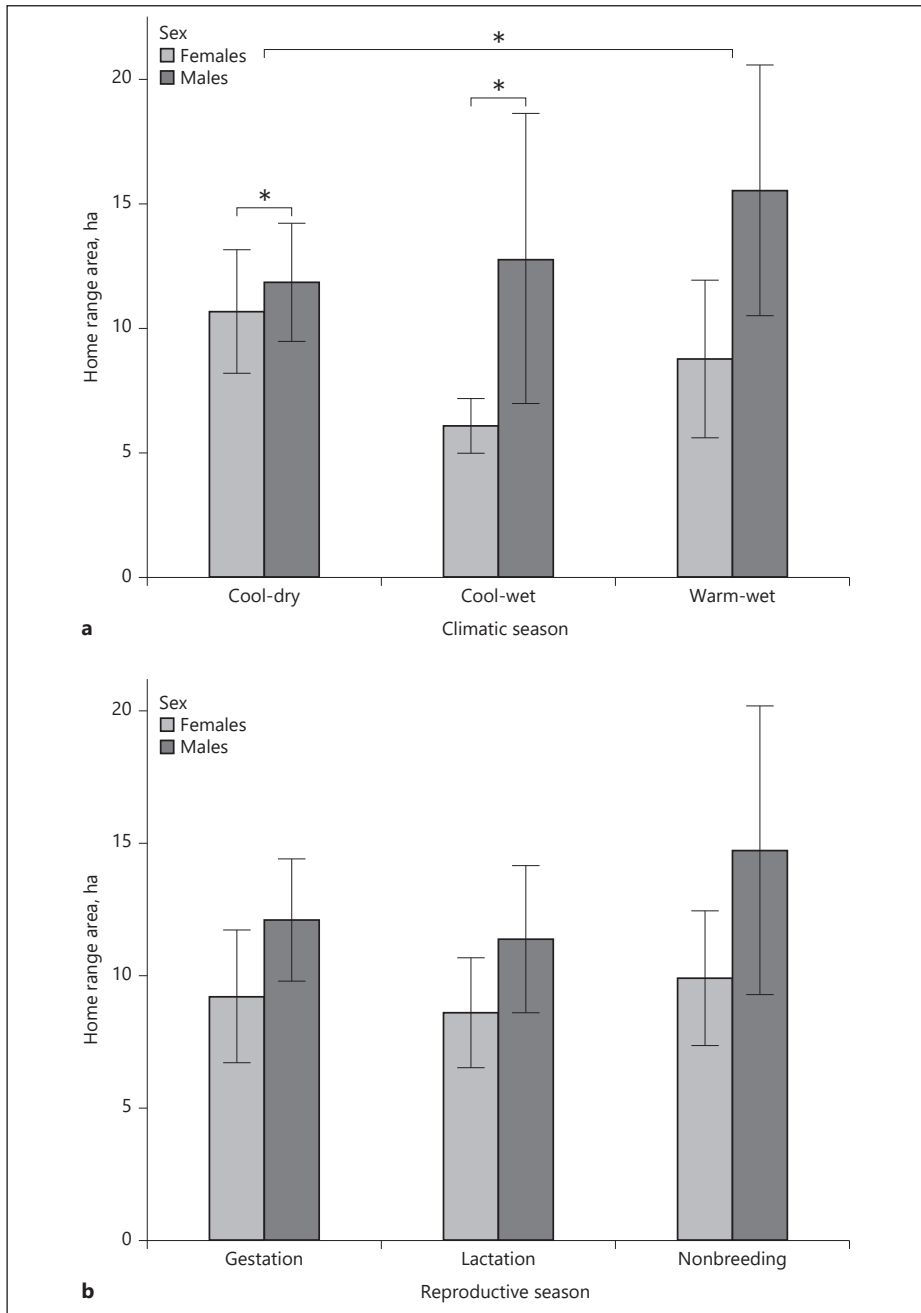
Fig. 4. Differences in home range area by sex and both climatic (**a**) and reproductive (**b**) seasons.
* *p* < 0.05. Male range use differed significantly across climatic seasons, using significantly small-
er home ranges than females during warm-wet and cool-wet seasons. Males' and females' home
range sizes did not differ significantly during the cool-wet period. By contrast, home range size
did not differ by sex across reproductive seasons.

Table 4. Models using a generalized linear mixed-effects model to estimate daily path length of *Varecia variegata* in the Mangevo community, a primary rain forest site within Ranomafana National Park, Madagascar

Model	K	AIC$_c$	ΔAIC$_c$	Model likeli-hood	Model weight (w_l)	Deviance
Reproductive season + day length + sex	13	5,721.53	0.00	1.00	0.88	5,695.53
Reproductive season + day length	7	5,725.53	4.00	0.14	0.12	5,711.53
Climatic season + day length + sex	17	5,745.85	24.32	0.00	0.00	5,711.85
Climatic season + day length	9	5,747.60	26.07	0.00	0.00	5,729.60
Day length	3	5,748.47	26.94	0.00	0.00	5,742.47
Climatic season + sex	9	5,749.19	27.66	0.00	0.00	5,731.19
Climatic season	5	5,750.87	29.34	0.00	0.00	5,740.87
Rainfall	3	5,754.58	33.05	0.00	0.00	5,748.58
(Null)	2	5,755.66	34.13	0.00	0.00	5,751.66
Sex	3	5,757.41	35.88	0.00	0.00	5,751.41
Rainfall + sex	5	5,757.79	36.26	0.00	0.00	5,747.79
Reproductive season	4	5,758.92	37.39	0.00	0.00	5,750.92
Infants + sex	4	5,759.45	37.92	0.00	0.00	5,751.45
Reproductive season + sex	7	5,761.00	39.47	0.00	0.00	5,747.00

Sampling occurred between 6 a.m. and 5 p.m. Fixed effects included day length, daily rainfall (mm), sex, presence of infants, climatic season, and reproductive season. To account for individual variation, "individual" was treated as a random effect. K indicates the number of model parameters. AIC$_C$, Akaike's information criterion with a small sample size bias correction.

Discussion

Previous work on wild ruffed lemurs has helped to characterize the genus *Varecia* as a taxon notable for its degree of social flexibility; populations exhibit striking variation in group size, social organization, and patterns of range use [reviewed in Vasey, 2003; Baden et al., 2016]. To some extent, this variation can be attributed to sample size, study duration and/or sampling method. However, even in long-term studies (>12 months of behavioral observation) populations have demonstrated remarkable variation in annual and seasonal fluctuations in demographics and behavior [Morland, 1991a, b; Rigamonti, 1993; Vasey, 2006; Baden, 2011].

Results from this study reveal mixed patterns of ruffed lemur range use, overlap, and daily distances traveled when compared with earlier work (e.g., *V. rubra* [Rigamonti, 1993; Vasey, 2006]; *V. variegata* [Morland, 1991a, b; Balko, 1998; Ratsimbazafy, 2002]; Table 5). We found that animals travel, on average, nearly 2 km per day. Multiple males and females exploit ranges that together comprise large, communal territories that are more or less spatially distinct from other neighboring social communities. Communal territory size was estimated at approximately 87 ha using KDE methods, though even with older MCP methods, our estimates fell well within the range of previously reported values (25–150 ha; reviewed in Vasey [2003]). Variations between our two size estimates, as well as among ours and earlier studies, are largely driven by the methods used to estimate home range area (MCP vs. kernel density) and should thus be taken into consideration when comparing range use across stud-

Table 5. Comparing results across published ruffed lemur studies

Species	Study site	Data collection	Analysis method	Population density/km²	Social organization	Group home range, ha	Group home range overlap	Female home range, ha	Male home range, ha	Individual range, ha	Individual range overlap	Sample size (adults), n	Study duration, months	Observation hours
Varecia rubra	Ambatonakolahy (Masoala)[1]	travel mapped during observations	Quadrats	21.5–23.3	fission-fusion	24.6	low	unk.	unk.	unk.	unk.	8 (4 females, 4 males)	11	704
Varecia rubra	Andranobe (Masoala)[2]	travel mapped during observations	MCP	31.2–53.4	fission-fusion	57.7	none	30.9	16.2	F > M	FF: high MM: none MF: high	8 (5 females, 3 males)	12	672
Varecia v ariegata	Nosy Mangabe[3]	sleep and feed trees mapped during observations	MCP	29–43	fission-fusion	30	low	unk.	unk.	unk.	FF: moderate? MM: moderate? MF: moderate?	14 (9 females, 5 males)	13	1,793
Varecia variegata	Vatoharanana (Ranomafana)[4]	unk.	unk.	unk.	dispersed monogamy	197	none	unk.	unk.	unk.	FF: n.a. MM: n.a. FM: high	2 (1 female, 1 male)	2	112
Varecia variegata	Vatoharanana (Ranomafana)[5]	travel mapped during observations	MCP	3	cohesive mm:mf	150	none	unk.	unk.	unk.	FF: high MM: high MF: high	5 (2 females, 3 males)	18	1,700
Varecia variegata	Valohoaka (Ranomafana)[5]	travel mapped during observations	MCP	6	cohesive mm:mf	100	none	unk.	unk.	unk.	FF: high MM: high MF: high	12 (5 females, 7 males)	18	1,700
Varecia variegata	Mangevo (Ranomafana)[6]	GPS coordinates (10-min)	MCP/ kernel	23.4	fission-fusion	120.4/87.8	low	26.3/ 16.9	17.5/ 13.8	F > M	FF: moderate MM: moderate MF: moderate	28 (13 females, 15 males)	12	4,000+
Varecia variegata	Manombo[7]	GPS coordinates (5-min)	MCP	0.25	dispersed mm:mf	30–70	none	unk.	unk.	F > M	FF: high MM: high MF: high	5 (3 females, 2 males)	18	1,431

MCP, minimal convex polygons; unk, unknown; n.a., not available. [1] Rigamonti, 1993. [2] Vasey, 1997, 2003, 2006. [3] Morland, 1991. [4] White, 1991. [5] Balko, 1998. [6] Baden, 2011; Baden et al., this study. [7] Ratsimbazafy, 2002.

ies. Generally, KDEs are more likely to capture the realized spatial distribution compared to MCPs, as they are more robust to outliers, and thus more appropriate for comparison [Powell, 2000; Laver and Kelly, 2008]. Because ours is the first study to employ the KDE method, we argue that our estimates likely reflect more conservative and perhaps more biologically meaningful measures of ruffed lemur range use compared to earlier work.

Neither sex ranged widely throughout the entire communal territory. Rather, both males and females concentrated their movement to only a fraction of the communal range. We report significantly different patterns of range use for males and females; males utilized home ranges that were, on average, 20% smaller than those of females. These results are largely consistent with sex-segregated patterns of range use described by Morland [1991a, b] and lend support to earlier studies describing females as being central to ruffed lemur social behavior [Morland, 1991a, b; Baden et al., 2016]. Our results differ, however, in that the individual ranges we observed were distributed evenly throughout the communal territory and both males and females exhibited on average moderate levels of annual home range overlap among both same- and mixed-sex dyads. This is in contrast to earlier reports describing males either as using small ranges that overlapped extensively with females, but which were discrete from (i.e., nonoverlapping with) other neighboring males [Vasey, 2006], or as ranging extensively and more widely than females throughout the entire community, and sometimes even into adjacent communities [Morland, 1991a].

Nevertheless, when considering all available data, broad patterns of ruffed lemur spatial dynamics emerge. It appears that ruffed lemur communities comprise large, multi-male, multi-female groups that live within a communally defended territory, particularly in populations exhibiting high levels of fission-fusion dynamics (e.g., Andranobe, Nosy Mangabe, Kianjavato, Mangevo) [Morland, 1991a, b; Vasey, 2006; Holmes et al., 2016; Baden et al., 2016, 2020]. Females consistently utilize larger annual home ranges than males, though range use – including DPL – appears to vary both within and between sexes dependent upon climatic season and reproductive state [Morland, 1991a, b; Vasey, 2006; this study]. Moreover, females are consistently described as being central to the formation of nuclear ("core") groups, both in terms of social interactions [Morland, 1991a, b; Vasey, 2006; Baden et al., 2016] and spatial association [Vasey 2006; this study].

Seasonal Variation in Range Size, Overlap, and Daily Distances Traveled
Beyond broad characterizations of annual home range size and overlap, we detected significant sex differences in ranging behavior across seasons. Interestingly, female home range size did not vary significantly by climatic (H1) or reproductive season (H2). Of 5 females for which we had comparable data across seasons, only 1 exhibited the expected patterns of home range size variation predicted for seasonal climatic shifts (i.e., largest ranges during warm-wet periods of resource abundance (P1.6); smallest ranges during cool-wet periods of resource scarcity (P1.3), as per Vasey [2006]); of the remaining 4 females, 2 used the relatively largest ranges during the cool-wet (i.e., resource poor) period, while the remaining 2 females exploited large and roughly equivalently sized home ranges in warm-wet (i.e., resource abundant) and cool-dry (i.e., moderate resource) versus cool-wet (i.e., resource poor) seasons (Table 3). Female range use was equally variable across reproductive seasons

(H2), and none met our expectations of home range size (P2.6, 2.9) or overlap (P2.7, 2.10).

Thus, it appears that sex differences in home range size variation were driven primarily by males, whose ranges varied significantly across climatic (H1) but not reproductive seasons (H2). Male range use did not, however, follow expected patterns. We predicted (P1.6) that home range size would be largest during the warm-wet, resource abundant period. Instead, male ranges were largest during the cool-dry period, and directly contradict earlier reports describing seasonal variation in range use as being driven exclusively by females [Vasey, 2006]. Rather, our results more closely align to those of Morland [1991a]. Males in our study consistently traveled longer daily distances than females (~1.9 vs. ~1.7 km/day), and daily female travel was constrained by reproductive state. Female DPL was consistent across nonbreeding and gestation periods (January to September, ~1.7 km/day) but decreased precipitously during the first 3 months following birth (October to December, ~0.8 km/day). Taken together, our results suggest sex-segregated patterns of range use in ruffed lemurs: females in the Mangevo ruffed lemur community used large, seasonally stable home ranges, but daily travel was constrained during the lactation period by the presence of dependent offspring. By contrast, males consistently traveled longer daily distances than females, but within smaller, more seasonally flexible areas. While unexpected, we propose a few hypotheses that may help to explain these patterns.

First, in many primate fission-fusion systems, the density and distribution of food resources impact patterns of spatial association [e.g., Lehmann and Boesch, 2005]. That female range use in this study did not vary according to climatic seasonality suggests that resources may have been evenly and/or abundantly distributed throughout the communal territory, and that female ranges each may have encompassed high-quality food. Alternatively, given the individual variation we observed, it could be that females in lower-quality territories adopted "time (energy)-minimizing strategies" by resting more and/or feeding on lower-quality food resources until conditions improved [see Tecot, 2008, for review]. Anecdotally, we found asynchronous fruit availability across female home ranges, even within the same feeding tree species [Baden, unpubl. data], suggesting this may be a valuable line of further inquiry. These and further investigations relating habitat structure and quality to individual patterns of activity and range use in the Mangevo ruffed lemur community are currently under way.

It is also possible that our use of "climatic season" was a poor proxy for resource availability. Although studies have found a direct relationship between rainfall and fruit availability in Madagascar [Overdorff, 1993; Meyers and Wright, 1993; Hemingway, 1996; Grassi, 2001; Dewar and Richard, 2007] – including earlier work at this site [Baden et al., 2016] – Ranomafana is particularly notable for its highly variable climatic conditions; annual rainfall, phenology, and the presence and duration of wet versus dry seasons vary considerably interannually [Wright et al., 2005]. Moreover, earlier work in the region and elsewhere has demonstrated that relationships between rainfall and fruiting patterns might not always exist [Tecot, 2008; Hemingway, 1998; van Schaik and Pfannes, 2005]. Nevertheless, the imperfect relationship between climate and phenology still cannot explain why males – but not females – exhibited seasonal variation in range use. It should be noted that while male range size varied significantly with climatic season, patterns were inconsistent with our expectations. If

males were, in fact, altering range use in accordance with resource availability and in accordance with the "time-minimizing" strategy of the species [Beeby and Baden, in review], we might expect larger home range sizes during resource rich months [e.g., Vasey, 2006]. However, male range size peaked during the cool-dry season, a period of low, but rising resource abundance, suggesting that males may not be modifying spatial patterns according to fruit availability. Instead, we argue that males may, instead, be mapping their ranges onto those of females (i.e., the limiting resource to males), as socioecological theory predicts [Sterck et al., 1997], particularly in the days during the cool-dry season that occur just prior to, during, and following the brief mating period. In support of this hypothesis, we observed a higher than average association among males and females according to female reproductive state [Baden et al., 2016]. Thus, it is possible that the observed variation in male home range size at Mangevo is actually a result of males expanding their otherwise small home ranges to map their range use on to those of female associates just prior to the brief mating period in late June through early July.

That male ranging patterns did not vary according to reproductive seasonality is therefore likely an issue of temporal scale in our analysis. Ruffed lemurs, as with other Malagasy primates, are characterized by strict seasonal breeding, and are generally only sexually receptive for 2–3 days during the year [Foerg, 1982; Brockman et al., 1987; Baden et al., 2013]. The brevity of estrus in ruffed lemurs therefore complicates seasonal home range estimates according to reproductive state, as it can be difficult to accurately identify the appropriate time frame for analysis. While our behavioral data recorded increased association between males and females during the "courtship" (prereceptive, nonbreeding) period (March to June) [Baden et al., 2016], these changes in behavior were not reflected in our ranging results. In fact, female-male kernel overlap was lowest during the nonbreeding season – a period that encompassed this early courtship phase. Unfortunately, we believe that our current temporal scale, which ranged from 3 to 5 months per "season," was simply too large to accurately reflect the shifting patterns of range use across these more fine-scale reproductive stages.

Similarly, we expected patterns of female range use to correspond more closely with reproductive state. Ruffed lemurs bear large litters of altricial young, and are notable for their shared nest use and communal infant care, particularly during the first several months after birth [Pereira et al., 1987; Morland, 1993; Vasey, 2007; Baden et al., 2013]. Because infants cannot cling and must instead be transported orally by mothers between nests, we expected female movement, and thereby home range size, to be constrained during the period of early lactation and high infant dependence. Moreover, we anticipated female ranges to exhibit greater overlap, a pattern which would have facilitated the communal infant care observed later in infant development (approx. 6–8 weeks) [Baden et al., 2013]. While patterns of association and DPL met expectations (i.e., females were significantly less social and daily distances traveled were more constrained during early stages of lactation and high infant dependence) [Baden et al., 2016; this study], home range area and overlap did not differ significantly from other reproductive seasons. Anecdotally, females traveled faster, took more direct routes, and regularly visited diverse areas throughout their range during this time [Baden, unpubl. data]. Thus, future studies will use newer and more nuanced methods (e.g., ctmm [Calabrese et al., 2016]; dynamic social network analyses [Blonder et al., 2012]) to further refine these results.

Finally, ruffed lemurs are "boom-or-bust" breeders, reproducing only during years when conditions allow [Ratsimbazafy, 2002; Baden et al., 2013]. Thus, it may be that patterns of home range area and overlap differ between breeding and nonbreeding years, and that the moderate overlap in home ranges observed during this study is actually high relative to years when females do not reproduce. This would also help explain reports of monogamy in the taxon if studies were conducted during nonreproductive years when animals are less social, group members are less cohesive and individuals use smaller, less overlapping home ranges [Baden, unpubl. data]. Future studies will attempt to document ruffed lemur ranging behaviors across boom and bust years to allow us to test this hypothesis.

Ruffed Lemur Range Use in Context

Earlier work has characterized ruffed lemurs as displaying a distinct pattern of fission-fusion dynamics that is both markedly different from and strikingly similar to haplorrhines with fluid fission-fusion grouping patterns [Baden et al., 2016]. Compared to haplorrhines, ruffed lemurs exhibit relatively smaller subgroup size, dramatically lower rates of association, and a female-centered social organization. Adult males and females are equally gregarious, sharing similar numbers of social partners (with the exception of adult male-male dyads [Baden et al., 2016]). Nevertheless, dyadic ruffed lemur social associations are generally sparse and weak, and average relatedness within the community is low [Baden et al., 2020]. Our present study further refines this characterization by adding a spatiotemporal component to our understanding of ruffed lemur fission-fusion dynamics. We found that males and females are more or less evenly distributed throughout a large, female-defended range, and while female home ranges are larger than males', group members exhibit equal and moderate home range overlap with other members of the community.

Thus, the available data suggest that ruffed lemurs do not adhere to the "female-bonded" community model as described for red ruffed lemurs from Andranobe [Vasey 1997, 2006] (Fig. 1), nor do they adhere to classic "male-bonded" or "bisexually bonded" community models exhibited by chimpanzees or spider monkeys, two other primates with high fission-fusion dynamics [reviewed in Lehmann and Boesch, 2005] (Fig. 1). Instead, results from this study describe a system that integrates aspects from both "bisexually bonded" and "female-bonded" community models. "Bisexually bonded" chimpanzee communities in West Africa (e.g., Taï [Lehmann and Boesch, 2005; Lemoine et al., 2019]; Bossou, Guinea [Sakura, 1994]) and spider monkeys in Yasuni [Spehar et al., 2010] tend to contain males and females that are equally gregarious and range together, with minor ranging differences between sexes due to differential usage of peripheral areas [Lehmann and Boesch, 2005]. Similar to these communities, male and female ruffed lemurs share strong bisexually bonded social associations [Baden et al., 2016], and sexes share similar and moderately overlapping home ranges [this study]. However, neither sex ranges widely throughout the communal range, instead concentrating their range use to small portions of the larger female-defended territory.

Moreover, although females are central to social relationships (i.e., female-female and female-male social associations are stronger than male-male associations [Baden et al., 2016]), as in the "female-bonded" ruffed lemur communities of Andranobe [Vasey, 2006], the smallest units of social and spatial organization in the Mangevo community are comprised of small nuclear units or "core groups" (sensu

Vasey, 1997), that comprise an adult male, female, and her predispersal aged young. Nuclear (core) groups have been found to preferentially associate and share space with each other more so than with members of other core groups [Baden et al., 2016, 2020]. In fact, recent work has found that social associations in this species are primarily driven by space use [Baden et al., 2020]. Home range overlap significantly predicts the strength of social interactions, more so than kinship, suggesting that neighbors are more likely to interact than even close relatives. Thus, taken together, the unusual patterns of range use and association described herein can best be characterized as a "nuclear neighborhood" (Fig. 1).

Most nuclear (core) groups in this study comprised an adult male and female pair. However, Radio-Red and Radio-Blue, females in the northern and southern neighborhoods, respectively, shared their ranges with an adult male, as well as with their subadult and adult offspring. In the case of Radio-Red, her offspring included two young males, as determined by their patterns of dental wear and body weights at the time of capture [Baden, unpubl. data], and were estimated to be no older than 2 years. Given that dispersal is unbiased in this species (i.e., both sexes disperse [Baden et al., 2014]), it is assumed that the males were approaching dispersal age and would soon leave in search of new territories. By contrast, although also determined to be a mother-offspring pair [Baden, 2011], Radio-Blue shared her home range with her adult daughter (Radio-Green). An earlier study suggests that ruffed lemur daughters may inherit their territory from their mother upon eviction or death [White 2009], similar to patterns observed in chimpanzees [Williams et al., 2002; Murray et al., 2008; Langergraber et al., 2009, 2013]. While it is not currently possible to assess home range inheritance at this time, Radio-Blue and Radio-Green resided in the same territory for at least 3 years prior to this study (since 2005), and remained in the territory together until at least 2011, lending anecdotal support for this hypothesis. Ongoing data collection efforts will soon allow us to investigate site fidelity as it relates to resource availability and distribution within this community, as well as the dynamics of home range turnovers after the occurrence of deaths from old age and/or predation events.

Nuclear (core) groups in this study were spatially organized into larger agglomerations of "neighborhoods" within the communal territory. The concept of "neighborhoods" is not new in the primate fission-fusion literature. For instance, although East African chimpanzees (*P. t. schweinfurthii*) generally conform to a "male-bonded" community model (i.e., females are generally less social than males and use much smaller, more stable ranges than male community members [Wrangham and Smuts, 1980; Williams et al., 2002]), several research groups have now described females as utilizing core areas that cluster spatially into neighborhoods within a larger male-defended range (Gombe [Wrangham and Smuts, 1980; Williams et al., 2002; Murray et al., 2008]; Kanyawara [Emery Thompson et al., 2007]; Ngogo [Wakefield, 2008; Langergraber et al., 2009, 2013]). In chimpanzees, the presence of "neighborhoods" [Williams et al., 2002; Emery Thompson et al., 2007; Murray et al., 2008; Wakefield, 2008; Langergraber et al., 2009] has been described as an outcome of male territory defense [Williams et al., 2002]. Theoretically, in the absence of males, the optimal female foraging strategy might be for chimpanzees to distribute themselves evenly across the landscape so as to feed and forage alone or in small groups where they have an intimate knowledge of food distribution. However, the territorial behavior of males renders the peripheries of communities unsafe for females [Hamai et al., 1992;

Arcadi and Wrangham, 1999; Williams, 1999; Watts and Mitani, 2000, 2001], thereby forcing them to cluster toward the center of the male-defended range [Williams et al., 2002]. By contrast, female ruffed lemurs tend to be dominant to males, and even then, rates of aggression within the species are very low [Overdorff et al., 2005]. It is therefore unlikely that the spatial organization of ruffed lemur neighborhoods is related to safety from members of adjacent communities. Rather, we hypothesize that ruffed lemur spatial organization is largely shaped by their ecology. In Gombe, steep valleys result in a patchy, heterogenous habitat, and female neighborhoods center around food-rich resources separated by intervening low-quality areas, suggesting that neighborhoods may be a product of the site's geography [Williams et al., 2002]. Anecdotally, community boundaries in Mangevo appear to segregate along mountain ridges, and researchers have suggested that both ruffed lemur communities and the neighborhoods within them may too be structured around the presence and distribution of valuable food resources [Baden, pers. observation].

Finally, neighborhood membership in chimpanzee females has significant implications for female reproductive success [Williams et al., 2002; Emery Thompson et al., 2007], with females in lower-quality neighborhoods having less access to preferred foods, lower ovarian hormone levels, and decreased infant survival [Emery Thompson et al., 2007]. How similar patterns of site quality relate to ruffed lemur behavioral ecology, reproductive physiology, and evolution remain to be seen but will provide countless valuable avenues for future research.

Statement of Ethics

We used remote anesthetization techniques to capture and collar study subjects following an established protocol [Glander, 1993]. Animal captures were performed by a team of skilled Malagasy technicians (Madagascar Biodiversity Partnership) in the presence of at least one trained veterinarian per capture season (Randy Junge, Felicia Knightly, Edward Louis, Angie Simai). A Dan-Inject (Brrkop, Denmark) model JM CO_2-powered rifle was used to administer 10 mg/kg estimated body weight of Telzaol® (Fort Dodge, LA, USA) via 9-mm (3/8") type "P" disposable Pneu-darts™ (Williamsport, PA, USA). GPS coordinates and trail headings were collected at the site of each capture, after which animals were transported back to camp for processing. During processing, subjects were monitored for heart rate, respiratory rate, and body temperature and were given a subcutaneous balanced electrolyte solution (lactate Ringer solution). Subjects were then allowed to recover from anesthesia in breathable fabric bags (~3 h) and then released at the site of capture. Any subjects who had not recovered prior to dusk were kept overnight and released at the capture site the following morning. Upon release, subjects were followed to ensure full mobility in trees and to confirm that there were no injuries as a consequence of the captures. All collars were well below the 5% threshold of the subjects' weight recommended for arboreal animals and were not observed to impede our subjects' normal behaviors.

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

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

A.L.B. conceived the project, collected data, analyzed data, and wrote the paper; J.O. contributed to data analysis and wrote the paper; B.D.G. analyzed the data and wrote the paper.

Appendix I

Our final data set included only those individuals for which we had sufficient sampling (i.e., location fixes) to estimate both annual and seasonal home range size and overlap. For annual home ranges, we included only those individuals for which we had at least 25 sampling days and 250 location fixes spread more or less evenly throughout the year (i.e., in 2 of 3 sampling seasons). For seasonal estimates, we included only those individuals for which we had at least 10 sampling days and 100 location fixes in at least one climatic or reproductive season. These criteria allowed us to include 100% of sampled females and 71% of sampled males in either annual or seasonal (or both) home range estimates; only 4 males were undersampled and therefore excluded from all further analyses.

Focal animal	Sex	Location days, *n*	Location points, *n*	Annual	Climatic season			Reproductive season		
					warm-wet	cool-wet	cool-dry	non-breeding	gesta-tion	lacta-tion
Pink-Yellow	F	26	385	–	X	–	–	–	–	–
Radio-Blue	F	90	4,277	X	X	X	X	X	X	X
Radio-Green	F	107	4,529	X	X	X	X	X	X	X
Radio-Orange	F	75	3,378	X	X	X	X	X	X	X
Radio-Red	F	92	3,958	X	X	X	X	X	X	X
Radio-Yellow	F	73	3,640	X	X	X	X	X	X	X
Red-Silver	F	32	532	–	X	–	–	–	–	X
Yellow-Green	F	21	332	–	X	–	–	–	–	X
Total individuals analyzed				5	8	5	5	5	5	7
Black-Blue	M	58	1,792	X	–	X	X	X	X	–
Black-Green	M	48	808	X	X	–	X	–	X	X
Blue-Yellow	M	12	331	–	–	–	–	–	–	–
Green-Orange	M	1	13	–	–	–	–	–	–	–
No collar	M	49	735	X	X	X	X	–	X	X
Purple-Orange	M	20	471	–	–	–	–	X	–	–
Radio-Black-Green	M	74	2,163	X	X	X	X	X	X	X
Radio-Blue-Orange	M	1	55	–	–	–	–	–	–	–
Radio-Purple-Silver	M	76	2,402	X	X	X	X	X	X	X
Red-Green	M	58	1,276	X	X	X	X	X	X	X
Red-Red	M	19	767	–	–	–	–	X	–	–
Yellow-Purple	M	56	1,600	X	–	X	X	X	X	–
Yellow-Red	M	28	542	–	–	X	–	–	X	–
Yellow-Yellow	M	2	14	–	–	–	–	–	–	–
Total individuals analyzed				7	5	5	6	5	6	5

Appendix II

Patterns of climatic, phenological, and ruffed lemur reproductive seasonality in Ranomafana National Park, Madagascar.

Season	Warm-wet		Trans. cool	Cool-wet			Cool-dry		Trans. warm	Warm-wet	
Fruit availability	peak[a,b,e]	peak[a,b,e]	lean[a–e]	lean[a–e]	lean[a–e]	lean[a–e]	lean[a–e]	rise[a,e]	rise[e]/peak[a,b]	rise[e]/peak[a]	peak[a,e]
Reproduction	Nonreproductive						Gestation		Lactation, nest, communal care		
Month	Jan	Feb	Mar Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec

[a] Phenological data from Overdorff [1993a, b]. [b] Phenological data from Balko [1998]. [c] Meyers and Wright [1993]. [d] Hemingway [1996, 1998]. [e] Baden, this study (unpubl. phenological data). Note: no infants were born in 2007, thus January–July 2008 were considered nonreproductive. In other years, this may be considered a continuation of lactation.

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