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Sex-segregated range use by black-and-white ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar.

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Short title: Ruffed lemur spatial ecology

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

Key words: home range, fission-fusion, daily path length, kernel density estimates, seasonality, nuclear neighborhood community model

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; Seyfarth et al., 2014; Perry, 2013], 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 [Williams et al., 2002; Symington, 1990; Chapman et al., 1995; Lehmann and Boesch, 2004; Mitani et al., 2002 and references therein], 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 non-human 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 [Otali and Gilchrist, 2006; Lehmann, and Boesch, 2008; Wrangham, 2000], and exhibit stronger social bonds with each other than either mixed-sex or female-female dyads [Machanda et al., 2013; Fedigan and Baxter, 1984; Gilby and Wrangham, 2008; Shimooka, 2003; Slater et al., 2009]. 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; Symington, 1990; Chapman, 1990; Lehmann and Boesch, 2008; Wrangham, 2000].

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 home ranges [Wrangham and Smuts, 1980; Symington, 1988b; Symington, 1990; Chapman and Wrangham, 1993; Williams et al., 2002; Shimooka, 2005; Wrangham et al., 1992; Nunes, 1995], and spend more time in the peripheries of their territory than do females [Chapman and Wrangham, 1993; Chapman, 1990; 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 [Chapman and Wrangham, 1993; Shimooka, 2005; Symington, 1988b; Nunes, 1995; Wrangham, 1979]. 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 & Boesch 2005; Fig. 1].

There is, however, notable inter- and intra-population variation in the patterns of association and range use observed in these species. For instance, some populations of chimpanzees (e.g., Bossou and Taiï 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 & 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 & 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 [Dolado et al., 2016, 2017; Izar et al., 2012; Ren et al., 2012] and/or in accordance with social variables such as subgroup size or the presence of sexually receptive mates [Ellis and Di Fiore, 2019; Dias and Strier,

2003; Bezanson et al. 2008; Strier, 2018]. 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 rainforests of Madagascar [Baden, 2011; Balko, 1998; Morland, 1991a; Rigamonti, 1993; Ratsimbazafy, 2002; Vasey, 2000]. Ruffed lemurs live in large social groups (e.g., 11 to 31 individuals) that are characterized by high levels of fission–fusion social dynamics [Holmes et al., 2016; Baden, 2011; Morland, 1991a,b; Rigamonti, 1993; Baden et al., 2016; Vasey, 1997]. 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, animals in primary rainforest 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 (e.g., [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 other females, and which encompassed the smaller, non-overlapping 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 nor 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 pre-mating period, when males traveled significantly farther than females in search of mates. As in an earlier study [Rigamonti 1993], animals were observed travelling 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 inter-population 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., Best et al., 2014; Carter et al., 2013; Frère et al., 2010; 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 daily path length within one *V. variegata* community during a one-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 non-human 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 & Dewar 1991; Wright 1999; Pereira et al. 1999; Dewar & 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 & 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) 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 cr eching 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 & subjects

Data presented here were collected from one black-and-white ruffed lemur (*Varecia variegata*) community at Mangevo bushcamp in Ranomafana National Park, Madagascar (RNP) during one year of observation (January - December 2008). Mangevo (21°22'60"S, 47°28'0"E) is a mid-elevation (660 - 1,200m) primary rainforest site within the southeastern parcel of RNP, 435 km² 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]).

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 - 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 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. 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 for that observation period. Observation periods ranged in duration between 8 to 11 hours 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 ($8.02 \text{ m} \pm 7.21 \text{ s.d.}$)—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].

We collected simultaneous data on subgroup location from the approximate group center at 10-minute 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). 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 dataset, 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, 2001; Kenward, and Hodder, 1996], 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 datasets described above, we estimated range use in two ways: using kernel density estimates (KDEs) and minimum convex polygons (MCPs). The first method, kernel density estimates (KDE) 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 x 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 datasets and when animals exhibit strong site fidelity [Hemson et al., 2005]. Given our large dataset and observations that animals regularly transverse 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, minimum convex polygons (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 [Laver and Kelly, 2008; Powell, 2000]. 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 UD's 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 & 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 & 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; 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 – February

2008; Cool-Wet/Fruit Scarcity: May-July 2008; and Cool-Dry/Low-to-Moderate Fruiting: August-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-June 2008; Gestation: July-October 2008; Lactation: November-December 2008) (Appendix II; see also Fig. 1 in [Baden et al., 2016]).

Daily range use

Finally, to gain a finer-scale understanding of daily range use, we calculated daily path lengths (DPL) for each individual as the sum of the Euclidean distances between consecutive GPS coordinates taken every 10-minutes. 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 0700 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 (AICc). To incorporate model selection uncertainty, we model-averaged all parameter estimates [Burnham and Anderson, 2002].

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 ha \pm 1.74 SD (KDE) to 26.3 ha \pm 4.50 SD (MCP), whereas an average male's home range was estimated to cover 13.04 ha \pm 0.98 SD (KDE) to 17.5 ha \pm 1.22 SD (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% - 21.8% of the total community home range (KDE: mean % of communal range = 19.2%, n = 5, range = 13.1 – 23.5%; MCP: mean % of communal range = 21.8%, n = 5, range = 11.3 – 32.2%), while males used between 11.5% - 15.7% (KDE: mean % of communal range = 15.7%, n = 7, range = 13.7 – 19.4%; MCP: mean % 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 dataset that broadly corresponded to nuclear ‘core groups’ of preferred male-female dyads (presumed mates) and mothers and their pre-dispersal 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 size 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 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 daily path lengths (DPL) (Mann-Whitney $U=9323.5$, $P=0.926$). Females traveled, on average, a daily distance of 1,659.28 m \pm 555.21 m whereas males traveled an average of 1,673.83 m \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 difference by reproductive season and day length; the model including the sex variable had seven times the support as the model without it (0.881 versus 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 hours of daylight, DPL in both the non-breeding season (female: 1761 \pm SE 57.6 m; male: 1948.6 \pm SE 122.0 m) and gestation seasons (female: 1736.1 \pm 99.48 m; male: 1917.0 \pm 296.8 m) were more similar than during lactation, when daily distances traveled by females (840.6 \pm SE 106.2 m) were far more restricted than males (1824.6 \pm SE 196.7 m).

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; Vasey, 2006; Rigamonti, 1993; 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., *Varecia rubra*: [Rigamonti, 1993; Vasey, 2006]; *Varecia 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 hectares using KDE methods, though even with older MCP methods, our estimates fell well within the range of previously reported values (25 to 150 hectares; reviewed in [Vasey, 2003]. Variation 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 studies. 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 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., non-overlapping 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 five females for which we had comparable data across seasons, only one 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 four females, two used the relatively largest ranges during the cool-wet (i.e., resource poor) period, while the remaining two 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 km vs. ~1.7km/day), and daily female travel was constrained by reproductive state. Female daily path length was consistent across non-breeding and gestation periods (January – September, ~1.7 km/day), but decreased precipitously during the first three months following birth (October – 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, unpublished 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 underway.

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 [Dewar and Richard, 2007; Grassi, 2001; Hemingway, 1996; Overdorff, 1993; Meyers and Wright, 1993]—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 inter-annually [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 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 thru 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 two to three days during the year [Brockman et al., 1987; Foerg, 1982; 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” (pre-receptive, nonbreeding) period (March-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 non-breeding season—a period that encompassed this early courtship phase. Unfortunately, we believe that our current temporal scale, which ranged from three to five 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 [Baden et al., 2013; Morland, 1993; Pereira et al., 1987; Vasey, 2007]. 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 (ca. 6-8 weeks; [Baden et al.,

2013]. While patterns of association and daily path length 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, unpublished data). Thus, future studies will use newer and more nuanced methods (e.g., ctm, [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 non-breeding years, and that the moderate overlap in home ranges observed during this study are 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 non-reproductive years when animals are less social, group members are less cohesive and individuals use smaller, less overlapping home ranges [Baden, unpublished 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., Tai: Lehmann & 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 & 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 pre-dispersal 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 female, her offspring included two young males, as determined by their patterns of dental wear and body weights at the time of capture (Baden, unpublished data), and were estimated to be no older than two years

old. 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 three 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., 2002b; Murray et al., 2008;

Kanyawara: Emery Thompson et al., 2007; Ngogo: Wakefield, 2008; Langergraber et al., 2009, 2013]. In chimpanzees, the presence of ‘neighborhoods’ [e.g., [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 & Wrangham, 1999; Williams, 1999; Watts & 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, personal 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.

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Statement of Ethics

We used remote anaesthetization techniques to capture and collar study subjects following 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 CO₂-powered rifle was used to administer 10mg/kg estimated body weight of Telazol® (Fort Dodge, LA) via 9 mm (3/8”) Type ‘P’ disposable Pneu-darts™ (Williamsport, PA). 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 (LRS, 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 (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Disclosure Statement

The authors have no conflicts of interest to declare.

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Author Contributions

ALB conceived of the project, collected data, analyzed data, and wrote the paper; JO contributed to data analysis, and wrote the paper; BDG analyzed the data and wrote the paper.

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

Hypotheses & 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 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 periods 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 periods 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 periods 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 cr�ching	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

Table 2. Individual annual home range area and overlap. Females used significantly larger home ranges than males (MCP: Mann-Whitney $U = 10.0$, $P = 0.04$; Kernel: Mann-Whitney $U = 9.0$, $P = 0.03$). However, sexes did not differ in their degree of home range overlap. Analysis includes individuals with ≥ 25 annual sampling days.

Collar ID	Sex	Located days	# location points	95% MCP (ha)	95% Kernel (ha)
RADIO-BLUE (rB)	F	90	4277	38.7	20.6
RADIO-BLUE-GREEN (rG)	F	107	4578	32.9	19.4
RADIO-ORANGE (rO)	F	75	3386	26.6	18.7
RADIO-RED (rR)	F	92	3960	19.6	14.1
RADIO-BLUE-YELLOW (rY)	F	72	3640	13.6	11.5
Female Mean		87.2	3968.2	26.3	16.9
BLACK-GREEN (BG)	M	48	808	22.8	17.0
NO COLLAR (NC)	M	49	735	18.3	13.8
RADIO-BLACK-GREEN (rBG)	M	74	2163	20.6	16.1
RADIO-PURPLE-SILVER (rPS)	M	76	2403	14.8	12.3
BLACK-BLUE (BB)	M	58	1792	14.9	12.0
RED-GREEN (RG)	M	58	1276	15.8	12.4
YELLOW-PURPLE (YP)	M	56	1607	15.0	12.7
Male Mean		59.9	1540.6	17.5	13.8
<i>p</i>				0.04	0.03
				Overlap	
		Sex-Sex	N dyads	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
<i>p</i>				0.62	0.70

Table 3. Average seasonal home range area and overlap between sexes. Comparisons include only those individuals with ≥ 10 sampling days per season and home range estimates from at least two of three seasons. Note that statistical comparisons were among only those individuals for which data were available from at least two of the three sampling periods.

A. Home range area (ha) by climatic season							
Sex	N	Warm-Wet	N	Cool-Wet	N	Cool-Dry	<i>p</i>
Females	8	15.53 ± 5.04	5	12.79 ± 5.82	5	11.84 ± 2.37	<i>ns</i>
Males	5	8.78 ± 3.17	7	6.08 ± 1.09	7	10.69 ± 2.48	*
<i>p</i>		*		*		<i>ns</i>	
B. Home range overlap (UDOI) by climatic season							
Overlap type	N	Warm-Wet	N	Cool-Wet	N	Cool-Dry	<i>p</i>
Female-Female	28	0.21 ± 0.36	10	0.11 ± 0.21	10	0.12 ± 0.06	<i>ns</i>
Female-Male	40	0.29 ± 0.46	35	0.31 ± 0.57	35	0.34 ± 0.54	<i>ns</i>
Male-Male	10	0.09 ± 0.27	21	0.30 ± 0.56	21	0.35 ± 0.75	<i>ns</i>
<i>p</i>		<i>ns</i>		<i>ns</i>		<i>ns</i>	
C. Home range area (ha) by reproductive season							
Sex	N	Nonbreeding	N	Gestation	N	Lactation	<i>p</i>
Females	5	14.76 ± 5.45	5	12.12 ± 2.30	7	11.40 ± 2.78	<i>ns</i>
Males	7	9.93 ± 2.55	8	9.24 ± 2.50	5	8.64 ± 2.07	<i>ns</i>
<i>p</i>		<i>ns</i>		<i>ns</i>		<i>ns</i>	
D. Home range overlap (UDOI) by reproductive season							
Overlap type	N	Nonbreeding	N	Gestation	N	Lactation	<i>p</i>
Female-Female	10	0.15 ± 0.30	10	0.12 ± 0.21	15	0.14 ± 0.32	<i>ns</i>
Female-Male	35	0.22 ± 0.39	40	0.33 ± 0.56	30	0.33 ± 0.62	<i>ns</i>
Male-Male	21	0.16 ± 0.36	28	0.33 ± 0.77	10	0.07 ± 0.18	<i>ns</i>
<i>p</i>		<i>ns</i>		<i>ns</i>		<i>ns</i>	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 4. Models using a generalized linear mixed-effects model to estimate daily path length of *Varecia variegata* in the Mangevo community, a primary rainforest site within Ranomafana National Park, Madagascar. Sampling occurred between 6am and 5pm. 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.

Model	K	AIC_c	ΔAIC_c	Model Likelihood	Model Weight (w_i)	Deviance
Reproductive season + day length + sex	13	5721.53	0.00	1.00	0.88	5695.53
Reproductive season + day length	7	5725.53	4.00	0.14	0.12	5711.53
Climatic season + day length + sex	17	5745.85	24.32	0.00	0.00	5711.85
Climatic season + day length	9	5747.60	26.07	0.00	0.00	5729.60
Day length	3	5748.47	26.94	0.00	0.00	5742.47
Climatic season + sex	9	5749.19	27.66	0.00	0.00	5731.19
Climatic season	5	5750.87	29.34	0.00	0.00	5740.87
Rainfall	3	5754.58	33.05	0.00	0.00	5748.58
(Null)	2	5755.66	34.13	0.00	0.00	5751.66
Sex	3	5757.41	35.88	0.00	0.00	5751.41
Rainfall + sex	5	5757.79	36.26	0.00	0.00	5747.79
Reproductive season	4	5758.92	37.39	0.00	0.00	5750.92
Infants + sex	4	5759.45	37.92	0.00	0.00	5751.45
Reproductive season + sex	7	5761.00	39.47	0.00	0.00	5747.00

Table 5. Table comparing results across published ruffed lemur studies.

Species	Study site	Data collection	Analysis method	Population density/km ²	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)	Study duration (months)	Observation hours
<i>Varecia rubra</i>	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
<i>Varecia rubra</i>	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
<i>Varecia variegata</i>	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
<i>Varecia variegata</i>	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
<i>Varecia variegata</i>	Vatoharanana (Ranomafana) ⁵	travel mapped during observations	MCP	5	cohesive mm:mf	150	None	unk.	unk.	unk.	FF: high MM: high MF: high	5 (2 females, 3 males)	18	1,700
<i>Varecia variegata</i>	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
<i>Varecia variegata</i>	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+
<i>Varecia variegata</i>	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

¹Rigamonti 1993; ²Vasey 1997, 2003, 2006; ³Morland 1991; ⁴White 1991; ⁵Balko 1998; ⁶Baden 2011; Baden & Gerber *this study*; ⁷Ratsimbazafy 2002

FIGURES





Community model	Male bonded	Bisexually bonded	Female bonded	Nuclear neighborhood
Description	Females occupy areas within a larger male-defended range; female core areas may or may not overlap	Males and females occupy a male-defended range; sexes share high core area overlap	Males occupy areas within a larger female-defended range; male core areas may or may not overlap	Nuclear groups of males & females occupy areas within a larger female-defended range; sexes share moderate home range overlap
Spatial model				
Predictions: HR size	M > F	M = F	M < F	M < F
HR overlap	MM overlap high FF overlap low FM overlap moderate	MM overlap high FF overlap high FM overlap high	MM overlap low FF overlap high FM overlap moderate	MM overlap moderate FF overlap moderate FM overlap moderate
References	Wrangham & Smuts 1980, Goodall 1986	Boesch 1996; Sakura 1994; Lehmann & Boesch 2005, 2008	Based on descriptions in Vasey 1997, 2006	This study

Figure 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.

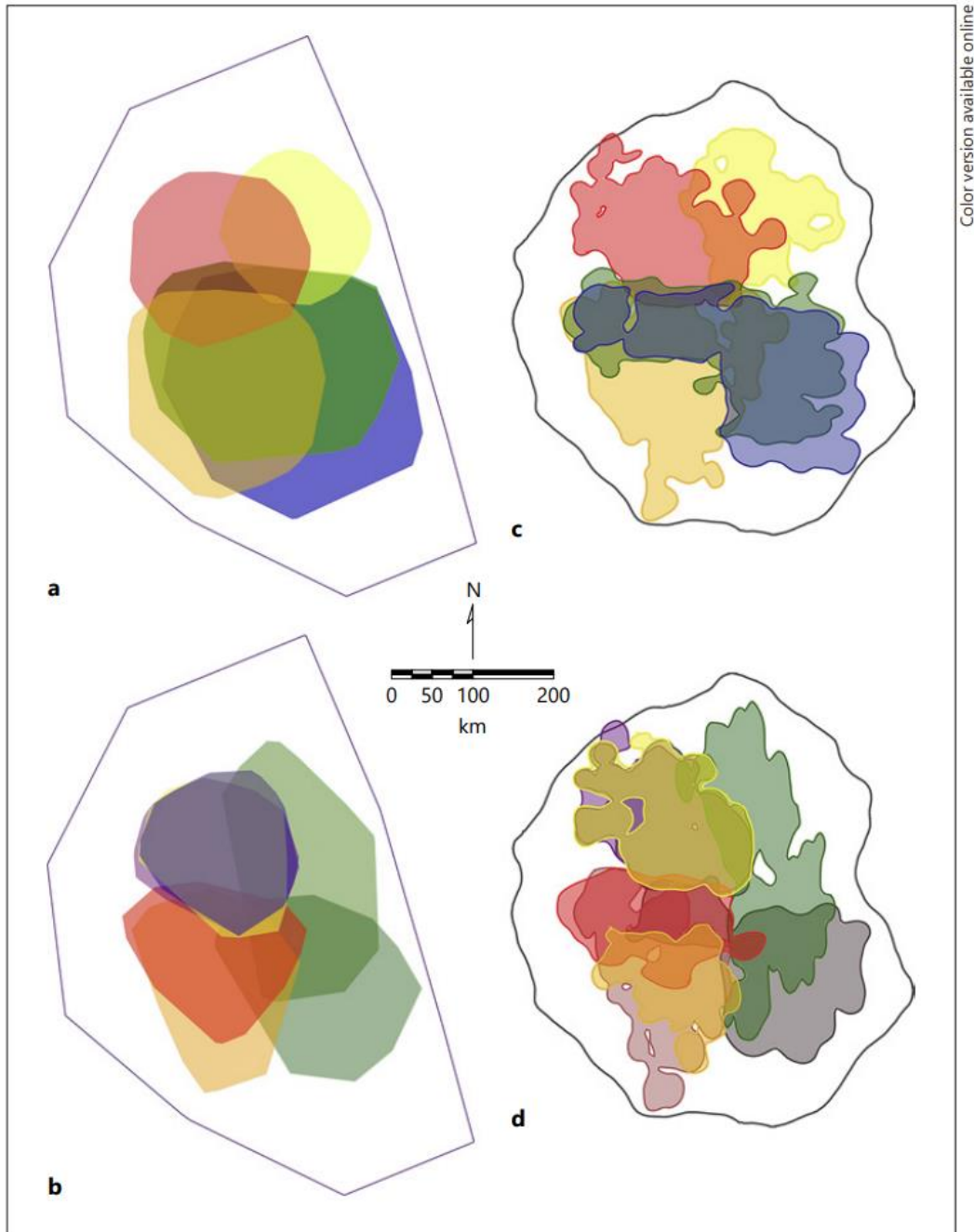


Figure 2. Differences in annual home range size and overlap for females (A & C, top, n=5) and males (B & D, bottom, n=8) using minimum convex polygon (MCP: A & B, left) and 95% kernel density estimates (KDE: C & D, right).

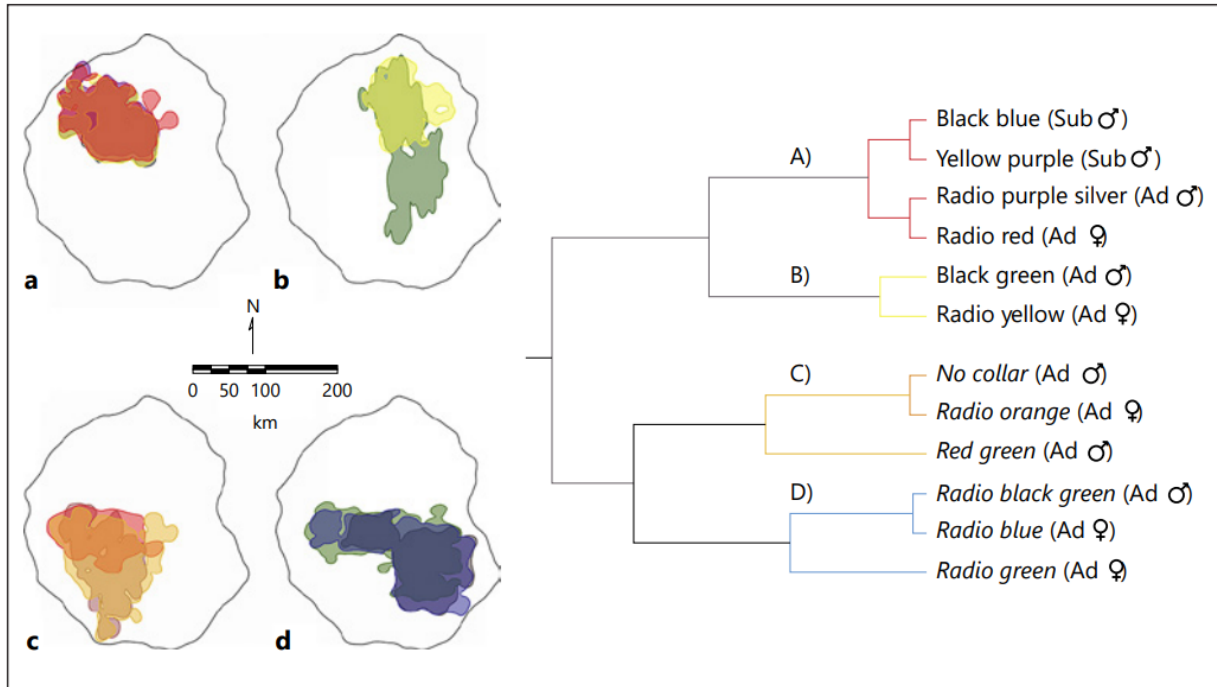


Figure 3. Nuclear (core) groups and neighborhoods as illustrated by overlapping 95% KDE estimates of annual home ranges (left) and the dendrogram resulting from hierarchical clustering analysis of averaged Euclidean distances between individual centers of range use (right) by members of the Mangevo ruffed lemur community. Nuclear groups are denoted by A-D (left & right). Regular text on the dendrogram indicates membership in the northern neighborhood; **bold italic** text indicates membership in the southern neighborhood.

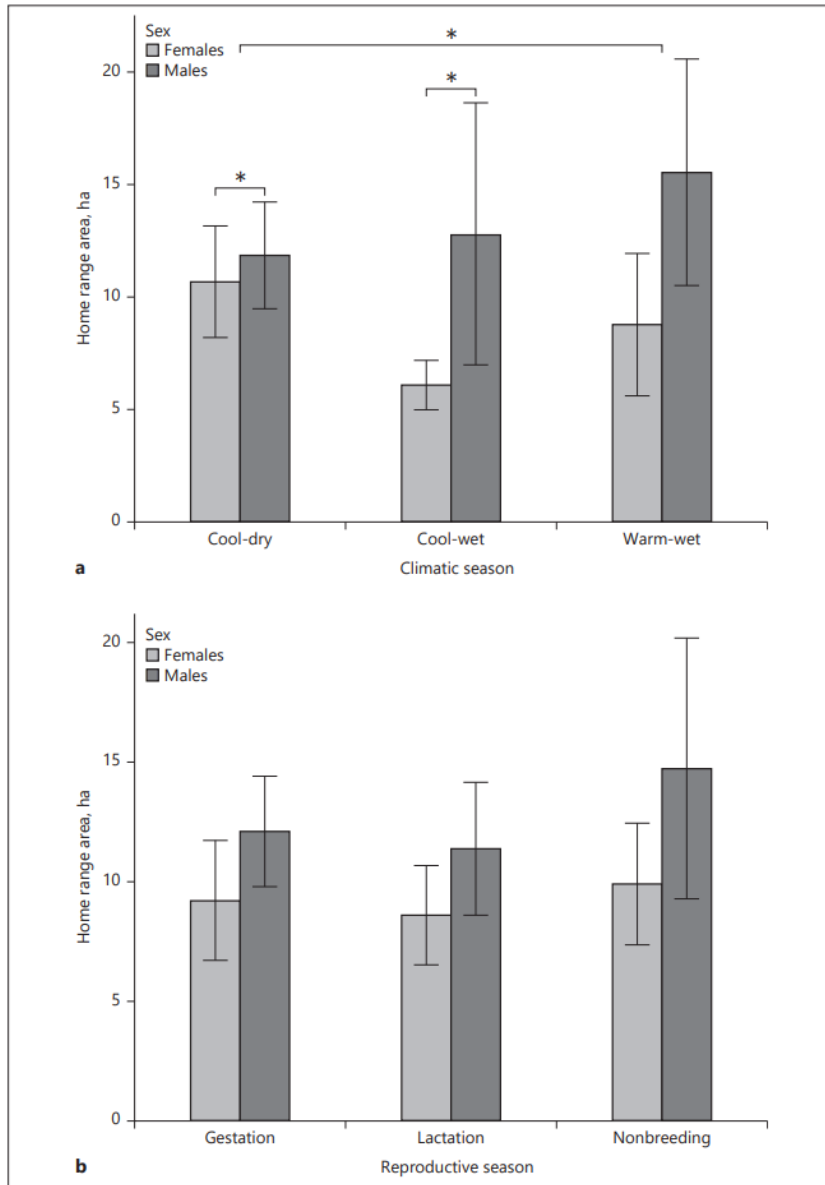


Figure 4. Differences in home range area by sex and both climatic (A) and reproductive (B) seasons. Male range use differed significantly across climatic seasons, using significantly smaller home ranges than females during warm wet and cool wet seasons. Males and females home range size did not differ significantly during the cool-wet period. By contrast, home range size did not differ by sex across reproductive seasons.