



Range utilization slopes as a measure of central tendency and intergroup overlap in primates

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Abstract

Animals that occupy stable home ranges tend to unevenly exploit different areas in their efforts to find fitness-limiting resources, while also reducing the risks of intergroup conflict. Most analyses of these extrinsic forces identify their effects on movement paths and home range geometry, but not on the interaction of these responses or how movements might be centrally constrained as a result of competition with neighbors. The range utilization slope is a measure of central tendency and consists of space use plotted against distance from the center of the range. Slopes tend to be linear, concave-up, or concave-down and are predicted to change as a function of feeding competition from neighbors. To test this prediction and determine the spatio-temporal scales over which the central tendency might vary, we calculated utilization slopes and an index of range overlap for grey-cheeked mangabeys (*Lophocebus albigena*), blue monkeys (*Cercopithecus mitis*), and red-tailed monkeys (*C. ascanius*) in Uganda, which consume similar diets but experience varying intensities of intergroup conflict. As predicted, we find variation in utilization slopes across and within species, which corresponds with the extent of range overlap among conspecific groups.

Significance statement

How animals use different parts of the home range provides clues to the constraints they experience, such as food availability, predation risk, and competition from neighbors. Despite its importance in behavioral ecology, the role that intergroup competition plays on home range geometry is not well understood. We propose that the range utilization slope, which evaluates spatial use as a function of distance from the center of the range, is a useful measure of central tendency and indicates how animals are compressed into the center of the range by neighbors. In an analysis of monkey groups of three species, we find that utilization slopes vary across space and time, but generally correspond with the intensity of resource limitation. These slopes provide a rapid assessment of resource access at multiple spatial scales.

Keywords Movement · Home range · Utilization distribution · Intergroup competition

Introduction

Movement behavior is an expression of the dynamic interface between an organism and its environment, and indicates the nature and strength of the intrinsic and extrinsic forces shaping its behavior (Turchin 1998; Nathan 2008). Movements reflect the need to find food and water (Noser and Byrne 2010); to avoid predators (Laundré et al. 2001); to access sleeping or nesting sites (Anderson 2000); to navigate around obstacles (Fahrig 2007); and to monitor, challenge, or avoid competitors over access to food resources (Brown and Waser 2018) and mates (Steenbeek 1999). Repeated pursuit of these goals within a home range results in over- and under-use of particular areas (Don and Rennolls 1983;

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Samuel et al. 1985). While much research has examined how landscape features, resource patterning, and predation risk shape space use (Schick et al. 2008), far less is understood about how these pressures are moderated by competition from conspecific neighbors (Waser and Wiley 1979; Minta 1992; Jetz et al. 2004), particularly for species in stable social groups within permanent home ranges (Abrahms et al. 2017). Moreover, much of what is known about neighbor relations focuses on face-to-face intergroup contests or responses to signaling behavior (Giuggioli et al. 2011; Markham et al. 2012), even though the competitive pressures exerted by neighbors affects space use well beyond these brief intergroup contacts (Brown and Crofoot 2013; Noonan et al. 2021) and is thought to shape broader patterns of habitat use (Wrangham et al. 2007).

Home ranges contain one or more “core” areas of intense use, and though the number and size of these areas depends strongly on the analytical method, their placement coincides with important feeding or sleeping sites (Powell 2000; Vander Wal and Rodgers 2012). Whereas the core is an area of heightened use, the periphery of the range is typically under-used. Neighboring ranges often overlap most extensively near the periphery, leading to rapid resource depletion and unpredictable food availability in this area (Tórrez-Herrera et al. 2020). Though patches of high-quality food may draw groups to peripheral overlap regions for brief periods (Wilson et al. 2012), use of these areas is generally suppressed in species that engage in highly aggressive and costly intergroup conflicts (e.g., chimpanzees, *Pan troglodytes*; Wilson et al. 2007). By avoiding the periphery, groups reduce their risk of injury, death, and other costs associated with these conflicts (Wrangham et al. 2007). In contrast, for species that exhibit non-lethal, low intensity, and frequent intergroup contests—as seen in species that defend home ranges using vocal, rather than physical, battles—groups use peripheral areas extensively (Robinson 1979).

It is useful to consider how space use varies between inner and outer parts of the range, as this approach reveals how groups respond to competitive pressure from neighbors. For instance, when a group is completely surrounded by neighbors and it defends the core area in order to maintain exclusive access to the food sources therein, the core should be positioned centrally in the home range—away from all competitors. Intense use of the center thus results in a negative relationship between use (per unit area) and distance from the center of the range. This center-to-edge slope is linear if the decline is monotonic but many groups are likely to deviate from this pattern, creating concave-up or -down slopes (Fig. 1), i.e., when the group spends a disproportionate amount of time within a relatively small portion of the home range, the resulting “utilization slope” has a concave-up shape. This pattern might arise if the risk of venturing

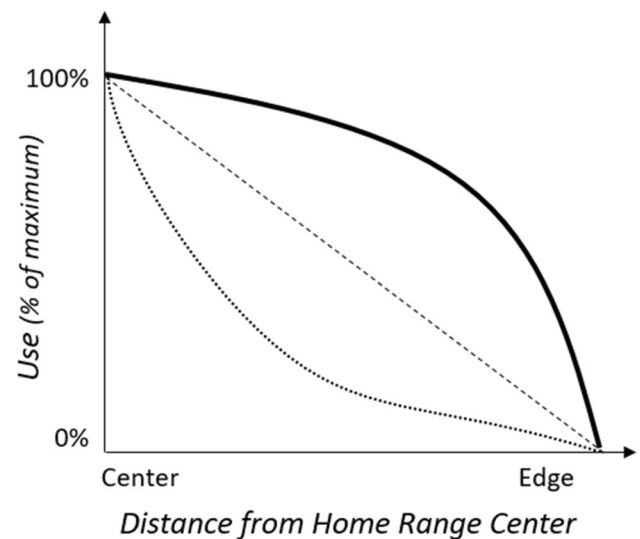


Fig. 1 Theoretical utilization slopes: concave-up (dotted line), linear (dashed line), and concave-down (thick solid line)

into the periphery greatly outweighs the benefits (Wrangham et al. 2007). Conversely, when the group concentrates its time within a relatively large central area, the result is a concave-down slope, which might arise when core areas are a relatively large portion of the home range (Vander Wal and Rodgers 2012). For both concave-up and -down slopes, there is an inflection point, and the intensity of use declines very steeply on one side of this point: when the negative portion of the slope is closer to the core, the result is a concave-up slope; when the negative slope is closer to the periphery, the result is a concave-down slope.

Quite unexpectedly, three primate species (chimpanzees, *Pan troglodytes*, and red-tailed monkeys, *Cercopithecus ascanius*, in Uganda and white-faced capuchins, *Cebus capucinus*, in Panama) with very different patterns of intergroup conflict and food defense all converge on a single pattern of dramatic under-use of the home range periphery (i.e., concave-up slopes; Wrangham et al. 2007). Aside from a fruit-based diet, there is no other obvious behavioral or physical commonality among these species that would account for their similar home range utilization slopes. Frugivory, however, does not necessarily account for their common space-use pattern; e.g., saki monkeys visit their peripheral areas as often (*Pithecia aequatorialis*; Van Belle et al. 2018) or more often (*P. irrorata*; Palminteri et al. 2016) than expected by chance. An alternative explanation points to the analytical method, which only evaluated narrow strips of land stretching in the four cardinal directions from the harmonic home range center (Wrangham et al. 2007). Heavily used central areas are over-represented on these strips, while any high-use peripheral areas are less likely to intersect with a strip because of the greater area of peripheral

regions. A fully inclusive analysis incorporating all parts of the home range is necessary to avoid the under-representation of peripheral areas.

Another explanation is that the original study populations (Wrangham et al. 2007) experience similar intensities of range compression due to the packing of group territories in the habitat (Brown 2013). In essence, concave-up slopes are a feature of populations in which conspecific home ranges overlap very little, so residents have sufficiently large and exclusive central areas and rarely make excursions into the outermost periphery of the home range. We predict that when group ranges overlap more extensively, the exclusive central areas are smaller and insufficient to feed the residents, necessitating frequent excursions into the periphery and resulting in concave-down utilization curves. In the absence of range overlap, the curve should flatten into either a negative linear slope, indicating that space use is solely a function of distance from the center and is unmodified by competitive pressures, or a horizontal slope, indicating no relationship between location and the intensity of space use. The combination of group density and range size indicates how much overlap exists among group home ranges and is thus one indicator of the intensity of intergroup competition. To enable comparison of range compression across sides of a home range shared with different neighbors, as well as across sites and species, Wrangham et al. (2007) created an index of range overlap (R_O). R_O is composed of the width of the home range (W) and the distance between centers of two adjacent ranges (D_R): $R_O = (W - D_R)/D_R$. Home ranges only

overlap when $R_O > 0$: when $R_O > 0$ but < 1 , the overlap is partial and groups maintain exclusive central areas; when $R_O > 1$, central areas are no longer exclusive. The three study populations in the original analysis all exhibited low R_O values (< 0.5) in addition to concave-up utilization curves.

Center-edge utilization slopes have not been examined in food-defending primates beyond the original analysis (Wrangham et al. 2007) so it is unclear whether these slopes are species-typical patterns or if, alternatively, they vary across populations, groups, years, or even across separate parts of a home range that face different neighbors. Moreover, the proposed relationship between utilization slopes and R_O has not been tested. To determine whether slopes are flexible and correspond with R_O , we analyze the space use patterns of three frugivorous monkey species at the Ngogo site in Kibale National Park, Uganda: six groups of red-tailed monkeys (*Cercopithecus ascanius*), two groups of blue monkeys (*C. mitis*), and five groups of grey-cheeked mangabeys (*Lophocebus albigena*; Table 1). These groups consume highly similar diets, use the same habitats (Struhsaker and Leland 1979; Conklin-Brittain et al. 1998; Brown 2013), and often travel and feed together (Cords 1990). Two species in the original analysis (chimpanzees and red-tailed monkeys; Wrangham et al. 2007) were studied at the Kanyawara site in Kibale National Park, which is approximately 15 km north-west of the location of the current study. To facilitate comparison across studies, we begin by using the same analytical methods as Wrangham et al. (2007) in which range use is examined along cardinal axes. We then extend

Table 1 Characteristics of the red-tailed monkey, grey-cheeked mangabey, and blue monkey group ranges at the Ngogo research site in Kibale National Park in Uganda. See text for derivation of home range width (W), distance between range centers (D_R), and range

overlap index (R_O). To enable comparison with results in Wrangham et al. (2007), home range size is calculated using minimum convex polygons (100% of points for red-tailed monkeys and 95% of points for mangabeys and blue monkeys)

Group	Observation years	Location points	Range size (km ²)	W (km)	Density (groups/km ²)	D_R (km)	R_O
Red-tailed monkey			0.490	0.790	5.55	0.456	0.73
R1	2008, 2013–2014	7237	0.488				
R2	2008, 2012–2015	10,378	0.584				
R3	2008, 2012, 2015	7946	0.500				
R4	2008, 2012–2014	4008	0.401				
R5	2011–2013, 2015	3737	0.474				
R6	2011–2013, 2015	3163	0.493				
Grey-cheeked mangabey			1.859	1.538	1.42	0.902	0.71
M1	2008–2009	11,294	1.933				
M2	2008–2009	9822	2.559				
M3	2008–2009	10,899	1.786				
M5	2008–2009	7938	1.838				
M6	2008–2009	4453	1.181				
Blue monkey			1.083	1.174	0.85	1.166	0.01
BN1	2015–2016	945	0.895				
BN2	2015–2016	1067	1.271				

the analysis by using a comprehensive method to examine center-edge utilization slopes by species, across groups, over time, and among varying sides of each home range (which face different neighboring groups) in order to identify the extent of variation in range use patterns. Finally, we calculate R_O for each species and compare these values to their utilization slopes.

Methods

Study site, species, and data collection

MB and a team of field assistants (the Ngogo Monkey Project) intermittently collected observational data from January 2008 through August 2016 at the Ngogo research station (0° 29' N 30° 25' E) in Kibale National Park (0° 13–41' N 30° 19–32' E), Uganda, during studies of the competitive regimes within each species (Table 1). Ngogo consists largely of old-growth rainforest intermixed with small patches of regenerating woodlands, riparian forests, and swamps (Struhsaker 1997).

Red-tailed monkeys and blue monkeys live in one-male, multi-female groups whereas mangabeys live in multi-male, multi-female groups (Struhsaker and Leland 1979); however, red-tailed monkey and mangabey groups are of similar sizes (Brown 2013) while blue monkey groups are considerably smaller (e.g., 4–9 individuals instead of the 10–19 individuals typical of red-tailed monkey and grey-cheeked mangabey groups; Brown 2013; Frogge et al. 2022). Red-tailed monkeys occupy much smaller home ranges than blue monkeys and grey-cheeked mangabeys (Table 1). Each group range contains a core area in which feeding, sleeping, and social activities are concentrated but primates differ from many other range-resident animals because this area is not the product of movements centered around a single nest or den (Burt 1943). Each study group is adjacent to 2–6 other groups, but only some of these neighbors were also study groups. All group members were habituated to the presence of human observers and were identified using a combination of features, including scars and other injuries, tail shape and color, nipple size and color in females, and the unique shape of the white nose spot in red-tailed monkeys.

As part of ongoing research by the Ngogo Monkey Project, monkey groups were followed from dawn until dusk for 5–14 consecutive days per month. In 2008–2009, 3–4 red-tailed monkey groups were followed simultaneously for 1 week each month and alternated with week-long follows of 3–6 grey-cheeked mangabey groups. In 2012–2015, pairs or trios of red-tailed monkey groups were observed for 1–2 weeks each month for periods of (mean $\pm$ SD) 4.9 $\pm$ 1.1 months ($N = 7$ periods), with 11–17 months between

successive periods in which a group was followed. The blue monkey groups were followed monthly from Aug 2015 through Aug 2016.

The field team recorded the centroid position of the majority of group members every 30 min using a 50 $\times$ 50 m gridded map of the trail system and by pacing to the nearest trails (2008–2015), or by using a hand-held GPS unit (2015–2016) and converting the UTM coordinates to the grid cell format. Location records for three additional groups of blue monkeys and one group of mangabeys were used to calculate group density but because these groups were followed for much shorter periods, we did not use their ranging data. It was not possible to record data blind because our study involved focal animals and groups in the field.

Data analysis

We began by replicating the approach used by Wrangham et al. (2007), in which utilization slopes are calculated using only those grid cells that radiate out from the home range center in the four cardinal directions (the mean $\pm$ SD percentage of cells in a home range that are included in these axes: red-tailed monkey = 17 $\pm$ 2%, blue monkey = 16 $\pm$ 1%, mangabey = 10 $\pm$ 2%). For each group, we calculated the center of the home range as the harmonic mean of the X and Y coordinates of all 30 min location scans. For each grid cell on the cardinal axes radiating outward from the harmonic center, we assigned a value for “distance,” from 0.0 (the center) to 1.0 (the outermost edge). Each cell was also assigned a value for “entries,” which was the number of times the group entered that cell. Inner cells are expected to be used more often than outer cells, so to standardize the cell entries such that the Y -intercept was at 1.0 (indicating maximum use), we divided each cell’s entries by the number of entries in the center cell. We then averaged across the four axes for each group, then averaged across groups within a species, and plotted the results (Fig. 2a). We visually compared the slopes against a diagonal line representing a 1:1 linear decline in use across the home range.

The limitations of the cardinal-axis approach described above are that most location points are ignored because they are not on a cardinal axis, and the harmonic means were far from the geographic centers of the ranges, resulting in highly asymmetrical axes. For instance, the cardinal axes for group B1 contained 5, 6, 12, and 16 cells. This asymmetry may explain the relatively jagged slopes that result from this analysis (Fig. 2a). Our second approach (hereafter referred to as the “all cells” method) was designed to rectify these issues. First, we included all cells in the home range rather than just those on a cardinal axis. Second, we determined the home range center and each cell’s distance from the center using a method in which we scored concentric layers of cells (Roth and Cords 2016): i.e., any outermost cell that

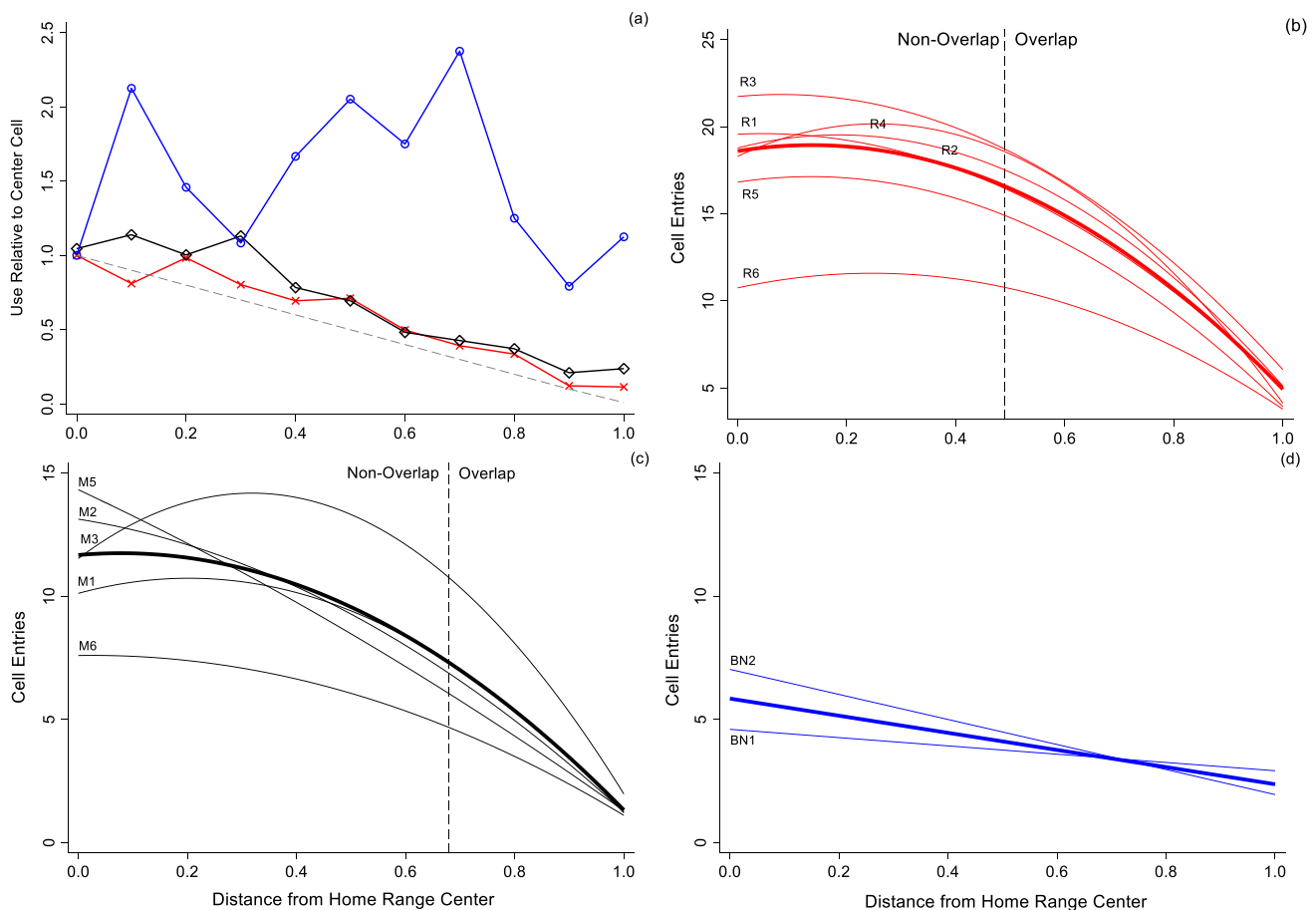


Fig. 2 Center-to-edge utilization slopes calculated for red-tailed monkeys (red lines and Xs, individual groups identified as R1–R6), grey-cheeked mangabeys (black lines and diamonds, groups M1–M6), and blue monkeys (blue lines and circles, groups BN1–BN2), using **a** the cardinal-axis approach and **(b–d)** the all-cells method. Dashed diagonal

line in **a** is the expected 1:1 relationship if cell use declined linearly from the center of the range. Dashed vertical line in **b, c** is the average extent of the overlap between adjacent home ranges. Thick lines in **b–d** are the mean response for each species. Slopes in **b–d** are model-fitted responses

was adjacent to unused areas outside the home range was labeled as layer 0; any cell that was an interior neighbor to a 0 cell was scored as layer 1, and each inner-neighbor cell is scored one higher than its lowest-valued neighbor (see Supplementary Fig. 1 in Roth and Cords 2016). We then flipped the layer numbers and divided by the total number of layers so that they ranged from 1.0 (outermost layer) to 0.0 (innermost layer). The result is a center layer rather than a point and this approach is optimal when location data are recorded using a grid rather than a GPS unit, as in this study. Any unused cells that were completely surrounded by used cells were included in the analysis.

We used a series of multilevel regression models to evaluate the relationship between space use and distance from the center of the home range, including all grid cells within the home ranges. We ran separate models for each species to avoid having to interpret interactions between species identity and each of the fixed effects described below. We ran two models per species because the entire set of fixed

and random effects could not be included in a single model, as doing so prevented it from reaching convergence. The response variable (“entries,” which is the number of times a group entered an individual 50 m × 50 m cell) is over-dispersed for red-tailed monkeys and mangabeys, but not blue monkeys, so we used a negative binomial distribution for the first two species and a Poisson distribution for the latter. The total number of observations (location points) per group was the offset term (referred to as an “exposure term” in STATA). The fixed effects included the linear and quadratic terms for distance from the home range center, generated with the “orthpoly” command in STATA (v12.1). If the center-edge utilization slopes are linear, the quadratic term will not be a significant predictor; if the slopes are concave-up or -down, the quadratic term will be significant and either positive or negative, respectively. To determine whether center-edge utilization slopes varied across sides of a home range that face different neighbors with varying competitive abilities, we calculated the cell’s bearing

(0–359°) relative to the unweighted mean position of the innermost layer of cells, and included the cosine and sine of the bearing as fixed effects to account for the circular nature of this predictor (Stolwijk et al. 1999). These “bearing” terms cannot identify specific neighbors but can give a general picture as to whether space use varies across different sides of a home range. Together, the variables for distance and bearing capture the spatial autocorrelation among adjacent grid cells.

In the first set of models (A), we included group identity as a random intercept to determine whether utilization slopes varied substantially among groups, which might arise if groups have distinct space-use tendencies or vary in dominance or other characteristics (Bode et al. 2011) not measured here. In addition, range size varies across groups and is likely to affect cell use; i.e., controlling for the number of location scans, groups with smaller home ranges should have a higher mean number of entries per cell than groups with larger ranges. We could not include range size and group identity simultaneously because this prevented the models from reaching convergence and/or computing predicted values, likely because the two predictors are equivalent (each home range size corresponded with only one group). In addition, we expected that neighboring groups might use a specific cell with similar intensity and thus cell identity should be included as a random intercept, but including cell and group identity as crossed random effects also prevented the models from converging. Thus, we created a second set of models (B) that differed from the first set as follows: the second set of models contained home range size as a fixed effect and omitted group identity in favor of cell identity as a random intercept. Comparing the relative strength of models A and B for each species using their AIC values (Burnham and Anderson 2002) allowed us to (1) distinguish whether potential inter-group differences in utilization slopes were due to varying home range size or to some other, unmeasured property of groups, and (2) determine whether the inherent value of a cell (e.g., its resources) was as strong a predictor of its use as its position within a particular home range.

Models A and B are designed to evaluate whether center-edge utilization slopes varied across species, groups, and sides of a home range. We included additional terms in the red-tailed monkey models to determine whether these slopes vary over time or if instead they exhibit within-group consistency in space use patterns. This analysis is ideal for red-tailed monkeys because we observed them across several distinct sampling periods over 5 years of observation (2008, 2012–2015), whereas the blue monkey and grey-cheeked mangabeys were observed in one period each. We divided the 2008 red-tailed monkey data into four chunks for comparison with the 2012–2015 periods, to allow for the possibility that range use might vary across seasons within

a year. We then calculated cell utilization per group, per observation period. We tested for a difference in the within- and between-group effects by including group means for the linear and quadratic distance terms as fixed effects (equation 3 in van de Pol and Wright 2009). We standardized all predictors in models A and B to facilitate comparison of effect sizes and conducted all regression analyses in STATA v17 (StataCorp LLC). Model results are reported as incidence rate ratios, where values > or < 1 indicate positive or negative effects, respectively.

We then calculated the index of range overlap (R_O) for each monkey species at Ngogo using population-averaged parameters, as in Wrangham et al. (2007). The distance between the centers of adjacent home ranges (D_R) is based on group density (G , measured as groups/km²) and the assumption of hexagonal packing of groups (Clark and Evans 1954): $D_R = \sqrt{2/(G * \sqrt{3})}$. We determined group density for each species using Biotas v2.0a 3.8 (Ecological Software Solutions LLC) by first calculating the 95% fixed kernel density polygon for each group and then calculating the percent of each home range that fell within a 1-km² square in the center of the study area and summing these percentages. The width of the average home range (W km) is calculated from its area (A km²) and is based on the assumption that ranges are generally circular: $W = 2 * \sqrt{A/\pi}$. Though not strictly true, it is a reasonable generalization for these populations because most groups had 5–6 neighbors surrounding them, and short-term fluctuations average out over multi-year periods and lead to rounded ranges (e.g., red-tailed monkey home ranges in Supplementary file 1, Fig. S1).

To visualize the degree of range overlap against the utilization slopes, we identified all cells within a home range that were shared with neighboring study groups, determined the minimum layer (i.e., distance from the innermost layer of cells) for each of these shared cells, and averaged this distance value for each species. The result was the average position within the home range where the overlap zone began. The benefit of this approach is that it allows us to extrapolate the total extent of shared area within a home range when ranging data are available for only some of the neighbors. From the average distance marking the beginning of the overlap zone, we then counted the number of cells within each home range that were at least that distance from the range center and calculated the area encompassed by the overlap zones.

Results

Unlike the patterns observed by Wrangham et al. (2007), none of the Ngogo monkey groups exhibited concave-up utilization slopes. When home range use is evaluated strictly

along the cardinal axes, all three frugivorous monkey species produced slopes mostly above the 1:1 expectation of declining use from the center to the edge of the home range (Fig. 2a). Using this method, red-tailed monkeys exhibit a roughly linear slope, grey-cheeked mangabeys a concave-down slope with a peak at 30% of the distance from the range center, and blue monkeys exhibit highly variable use of the home range. The uneven patterns for blue monkeys may be a product of the fact that cell use is scored relative to the use of the harmonic mean center cell, which was used relatively infrequently, and the cardinal axes within each home range differed in length.

Our alternative method of scoring range use—in which we consider all cells within the home range, identify a central layer rather than a point, and use a regression model to evaluate the slope—also shows variation in center-edge utilization slopes across species but yields slightly different patterns than the Wrangham et al. (2007) method. The all-cells method indicates that both red-tailed monkeys and grey-cheeked mangabeys exhibit concave-down utilization curves, whereas blue monkeys exhibit negative linear slopes (Table 2, Fig. 2b–d).

For all three study species, the AIC score of model B was substantially lower than model A (compare Table 2 with Supplementary file 1, Table S1), signaling that cell identity and/or range size accounted for more variation in cell use than group identity. As a result, the intergroup differences in center-to-edge utilization slopes (Fig. 2b–d) are due largely to variation in range size and were generally similar to the overall slope for the species. As predicted, each cell was entered less often,

on average, in a larger home range than in a smaller range. The “bearing” terms indicate that cell use varied substantially across different sides of the home range for mangabeys (Supplementary file 1, Fig. S2a), varied slightly within red-tailed monkey home ranges (Supplementary file 1, Fig. S2b), and not at all for blue monkeys (Table 2).

We sampled red-tailed monkeys across several years, which allowed us to determine not only whether groups exhibited consistent differences in their utilization slopes (a between-subject effect), but also whether the utilization slope for a group was consistent over time (a within-subject effect) and if there were meaningful differences in the direction and magnitude of these effects (van de Pol and Wright 2009). The non-significant “group mean” terms (Table 2) indicate no difference in the direction or magnitude of the between- and within-subject effects.

The index of range overlap (R_O) corresponded with the shape of the center-edge utilization slope in all species studied to date (Fig. 3): $R_O \approx 0$ for groups with a linear slope (blue monkeys); $0 < R_O < 0.25$ for groups with concave-up slopes (from Wrangham et al. 2007); and $R_O > 0.70$ for groups with concave-down slopes (red-tailed monkeys and grey-cheeked mangabeys). Increasing R_O corresponds with more steeply negative slope coefficients (from Table 2), indicating a more curvilinear response. The mean distance from the home range center where the overlap zone began was 0.49 and 0.68 for red-tailed monkeys and grey-cheeked mangabeys (vertical dashed line in Fig. 2b, c); thus, the overlap area accounted for 79% and 73% of the total home range area for each species, respectively.

Table 2 Regression models examining the predictors of grid cell use as a function of distance from the center layer of the home range (model B). *IRR*, incidence rate ratio. Significant predictors ($\alpha \leq 0.05$) are indicated in bold font

Species	Red-tailed monkey	Grey-cheeked mangabey	Blue monkey
<i>N</i> (group cells)	3611	3187	582
Wald χ^2	1460	2777	71.49
<i>P</i>	< 0.001	< 0.001	< 0.001
AIC	22,939	15,036	2562
Variables	IRR (95% CI)	IRR (95% CI)	IRR (95% CI)
Distance-linear	0.61 (0.60, 0.63)	0.48 (0.46, 0.49)	0.78 (0.73, 0.83)
Distance-quadratic	0.83 (0.81, 0.84)	0.74 (0.72, 0.76)	0.97 (0.91, 1.03)
Bearing-cosine	0.89 (0.79, 1.00)	1.40 (1.24, 1.59)	1.12 (0.83, 1.51)
Bearing-sine	0.92 (0.82, 1.04)	1.29 (1.14, 1.45)	1.01 (0.75, 1.36)
Range size	0.05 (0.04, 0.07)	0.81 (0.79, 0.84)	0.96 (0.90, 1.03)
Group mean-linear	1.00 (0.97, 1.03)	-	-
Group mean-quadratic	0.97 (0.94, 1.00)	-	-
Intercept	0.0004 (0.0003, 0.0006)	0.001 (0.001, 0.001)	0.003 (0.0026, 0.0030)
Log (alpha)	- 0.86 (- 0.93, - 0.80)	- 1.36 (- 1.51, - 1.20)	-
Random effect	Variance (95% CI)	Variance (95% CI)	Variance (95% CI)
Intercept: cell	0.14 (0.11, 0.17)	0.21 (0.17, 0.25)	0.29 (0.23, 0.37)

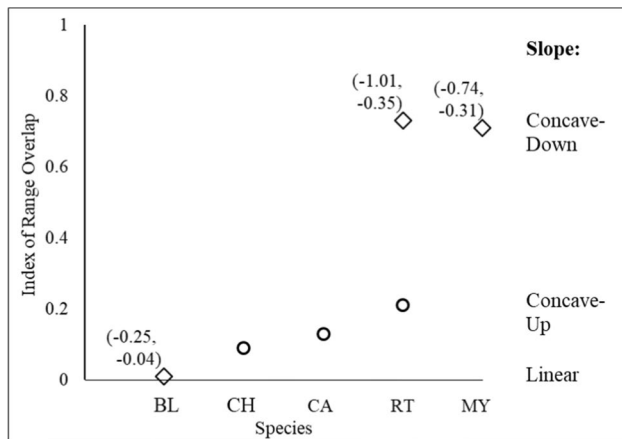


Fig. 3 Utilization slopes and range overlap for primate species studied at Ngogo (hollow diamonds) or by Wrangham et al. (2007; hollow circles). Species abbreviations: BL, blue monkey; CH, chimpanzee; CA, white-faced capuchin; RT, red-tailed monkey; MY, grey-cheeked mangabey. Coefficients of the (linear, quadratic) “distance” predictors from model B (back-calculated from the incidence-rate ratios in Table 2) are given in parentheses above each Ngogo species

Discussion

As we predicted, all three primate study species used areas in the center of the home range more intensively than peripheral areas, but we also found substantial variation in the shape of the center-to-edge utilization slopes across species, groups, and sides of the home range. The slopes for the species studied here (concave-down and linear) differ from those of an earlier study (concave-up; Wrangham et al. 2007), which is particularly notable considering that each analysis included red-tailed monkey groups from the same national park in Uganda. This intraspecific variation is not attributable to the analytical method: we used both the original cardinal-axis technique as well as a more comprehensive statistical model and in neither case did we find concave-up utilization curves for the Ngogo red-tailed monkey groups. Most striking is the discovery that utilization slopes appear to correspond with the extent to which neighbors intrude into one another’s home ranges, expressed as the range overlap index. These results confirm that primates can express diverse patterns of range use, which correspond with the competitive pressures exerted by neighboring groups in areas of home range overlap. Previous modeling demonstrated that range overlap and intergroup feeding competition affects the size of the home range (Jetz et al. 2004), but our results extend this relationship by examining the extent to which movements are concentrated in the center of the range.

Though each species is characterized by a distinct center-to-edge utilization slope, there is also variation among and within groups. The intraspecific variation arises not just

from different patterns of space use, but from home range and sample size. It is unclear why mangabey and red-tail utilization slopes vary across sides of the home range, but blue monkey slopes do not. One possibility points to varying resource availability: controlling for distance from the range center, locations with greater resource abundance might be over-used relative to areas with lower food availability (Samuel et al. 1985). While intuitive, this explanation seems unlikely because the blue monkey group ranges were closely aligned with two mangabey home ranges (Supplementary file 1, Fig. S1) and thus should have shown the same patterns if slopes were determined solely by resource availability. Alternatively, variation in range use across home range sides may correspond with characteristics specific to the group rather than the landscape (Morales and Ellner 2002), such as intergroup dominance (Markham et al. 2012; Roth and Cords 2016). In other words, dominant and subordinate groups range differently on their respective home range sides, indicating larger and smaller central areas of intense use. To test this idea, further analysis is necessary to determine (1) whether the patterning of intergroup encounters predicts side-specific utilization slopes by adjacent groups and (2) if both mangabeys and red-tailed monkeys express intergroup dominance.

The center-edge utilization slope combines information about relative location and the intensity of use, which means it is a simplified, one-dimensional representation of a utilization distribution (Worton 1989). The usefulness of this measure is that it facilitates comparison of spatial patterns at many scales—e.g., across species, groups, observation periods, or portions of a home range. Whereas previous analyses of intergroup dynamics in movement ecology have focused on encounter rates and locations (Noonan et al. 2021), the center-to-edge utilization slope moves beyond direct encounters and incorporates all of the ways—both direct and indirect—in which neighbors affect each other (Brown and Crofoot 2013). Its correspondence with the packing of groups in the habitat (R_0) supports the interpretation that the intensity of competition with neighbors influences not only the size of the home range and the overlap area (Pearce et al. 2013), but the degree to which group movements are compressed within the range, away from neighbors. In a low-density population like the Ngogo blue monkeys, neighboring ranges rarely overlap, and the result is a negative linear utilization slope; this pattern indicates that even in the absence of intergroup competition, central areas of the home range are used more often than peripheral areas. This pattern could arise from a greater abundance (Harris 2006) of resources in the center of the home range, as an artifact of frequent diagonal movements across the range (Seaman and Powell 1990), or from a tendency to return to remembered areas (Van Moorter et al. 2009). When intergroup competition is

sufficiently intense, the negative linear slope is deformed into a concave-up or -down curve. These curves, in which activity is concentrated in the inner portion of the home range, produce similar patterns as those seen in “central-place forager” and “territorial” movement syndromes (*sensu* Abrahms et al. 2017). The intraspecific variation in movement patterns documented here implies that these two systems lie on a spectrum of range use, with groups exhibiting more or less of a centralized tendency as a result of varying competitor pressure. Notably, some study groups had core areas that were not centrally positioned in the home range (Supplementary file 1, Fig. S1), yet still showed negative slopes, indicating greater use of inner layers. This pattern indicates that the utilization slopes method is robust to variation in home range geometry.

Though the groups with concave-up curves (from Wrangham et al. 2007) had lower range overlap indices than the groups with concave-down curves (Fig. 3), this does not mean they experienced less feeding competition or higher energy gain; instead, they may actually experience more intense pressure from neighbors. Consider the red-tailed monkey populations: Kanyawara groups are larger (mean = 20.3 adults, $N = 3$ groups; Bryer 2020) than at Ngogo (mean = 12.8 adults, $N = 6$ groups); Kanyawara groups live in home ranges that are less than half the size of the Ngogo ranges, and group density is higher at Kanyawara than at Ngogo (compare Table 1 with Wrangham et al. 2007); and food abundance is lower at Kanyawara than at Ngogo (Chapman et al. 1999; Potts et al. 2009). We infer from these patterns that resource limitation and feeding competition may be more intense at Kanyawara than at Ngogo. Further study is needed to test whether groups with tightly centralized movement patterns (concave-up utilization curves) and low overlap are in poorer energetic condition than groups with broader central tendencies (concave-down curves) and high overlap. It might seem counterintuitive that communities with less overlap among groups fare worse than communities with extensive overlap. This pattern is not uncommon, though, because as resource limitation intensifies, range size decreases, and groups make more of an effort to evict neighbors from the home range, creating a more formal territorial boundary (Pearce et al. 2013).

Due to the importance of linking behavioral responses to patterns of competition and resource availability in a rapidly changing world, there is a pressing need to develop, test, and implement indices like the center-to-edge utilization slope, which is constructed solely from location data. Ranging behavior is far easier to track than measures of food availability (particularly for animals like primates, which have varied and flexible diets), energetic condition, and reproductive success. If the proposed connection to resource limitation is correct, this index would greatly simplify and standardize attempts to measure the health of wild populations.

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Author contribution MB oversaw collection of the data in the field, designed the study, conducted the statistical analyses, and co-wrote the manuscript. MRG collated and prepared the data for analysis and co-wrote the manuscript.

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Data availability The raw movement datasets used for the current study are available via MoveBank (www.movebank.org): study name “NMP Ngogo Monkeys (redtail, mangabey; 2008–2009)” and study ID 1141207728; study name “NMP Ngogo Monkeys (redtail, 2012–2015)” and study ID 1142094968; study name “NMP Ngogo Monkeys (blue, mangabey; 2015–2018)” and study ID 1142311460. The aggregated movement datasets analyzed during this study are publicly available from Data Dryad: <https://doi.org/10.25349/D9J61Z>.

Declarations

Ethics approval Permission to carry out this study was granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the Uganda Office of the President. The protocols were approved by the Institutional Animal Care and Use Committees (IACUC) of Columbia University (AC-AAA8112) and the University of New Mexico (11-100661-MCC) and deemed exempt at the University of California, Santa Barbara. All research activities were conducted in compliance with Ugandan national laws, in adherence with the ASAB/ABS Guidelines for the Use of Animals in Research, and all institutional guidelines. The non-invasive field observations were conducted exclusively within Kibale National Park, a public entity managed by the Uganda Wildlife Authority. The IUCN conservation status of red-tailed monkeys, blue monkeys, and grey-cheeked mangabeys is “least concern,” and no monkeys were handled, captured, or otherwise manipulated during this study.

Conflict of interest The authors declare no competing interests.

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References

- Abrahms B, Seidel DP, Dougherty E et al (2017) Suite of simple metrics reveals common movement syndromes across vertebrate taxa. *Mov Ecol* 5:1–12. <https://doi.org/10.1186/s40462-017-0104-2>
- Anderson JR (2000) Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Med Rev* 4:355–373. <https://doi.org/10.1053/smr.2000.0105>
- Bode NWF, Wood AJ, Franks DW (2011) The impact of social networks on animal collective motion. *Anim Behav* 82:29–38. <https://doi.org/10.1016/j.anbehav.2011.04.011>
- Brown M (2013) Food and range defense in group-living primates. *Anim Behav* 85:807–816. <https://doi.org/10.1016/j.anbehav.2013.01.027>
- Brown M, Crofoot MC (2013) Social and spatial relationships between primate groups. In: Sterling E, Bynum E, Blair M (eds) *Primate ecology and conservation: a handbook of techniques*. Oxford University Press, Oxford, pp 151–176 <http://link.springer.com/article/10.1007%2Fs10764-014-9762-8>
- Brown M, Waser PM (2018) Group movements in response to competitors' calls indicate conflicts of interest between male and female grey-cheeked mangabeys. *Am J Primatol* 80:e22918. <https://doi.org/10.1002/ajp.22918>
- Bryer MAH (2020) Nutritional strategy and social environment in red-tail monkeys (*Cercopithecus ascanius*). Dissertation, City University of New York, https://academicworks.cuny.edu/gc_etds/3554
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York
- Burt WH (1943) Territoriality and home range concepts as applied to animals. *J Mammal* 24:346–352. <https://doi.org/10.2307/1374834>
- Chapman CA, Wrangham RW, Chapman LJ et al (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J Trop Ecol* 15:189–211. <https://doi.org/10.1017/S0266467499000759>
- Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453. <https://doi.org/10.2307/1931034>
- Conklin-Brittain NL, Wrangham RW, Hunt KD (1998) Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int J Primatol* 19:971–998. <https://doi.org/10.1023/A:1020370119096>
- Cords M (1990) Mixed-species association of East African guenons: general patterns or specific examples? *Am J Primatol* 21:101–114. <https://doi.org/10.1002/ajp.1350210204>
- Don B, Rennolls K (1983) A home range model incorporating biological attraction points. *J Anim Ecol*:69–81. <https://doi.org/10.2307/4588>
- Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. *Funct Ecol* 21:1003–1015. <https://doi.org/10.1111/j.1365-2435.2007.01326.x>
- Frogge H, Jones RA, Angedakin S et al (2022) Constraints on population growth of blue monkeys (*Cercopithecus mitis*) in Kibale National Park, Uganda. *Behaviour* 159:961–987. <https://doi.org/10.1163/1568539X-bja10160>
- Giuggioli L, Potts JR, Harris S (2011) Animal interactions and the emergence of territoriality. *PLoS Comput Biol* 7:e1002008. <https://doi.org/10.1371/journal.pcbi.1002008>
- Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). *Behav Ecol Sociobiol* 61:317–329 <http://www.jstor.org/stable/25511584>
- Jetz W, Carbone C, Fulford J et al (2004) The scaling of animal space use. *Science* 306:266–268. <https://doi.org/10.1126/science.1102138>
- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Can J Zool* 79:1401–1409. <https://doi.org/10.1139/z01-094>
- Markham AC, Alberts SC, Altmann J (2012) Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population. *Anim Behav* 84:399–403. <https://doi.org/10.1016/j.anbehav.2012.05.009>
- Minta SC (1992) Tests of spatial and temporal interaction among animals. *Ecol Appl* 2:178–188. <https://doi.org/10.2307/1941774>
- Morales JM, Ellner SP (2002) Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* 83:2240–2247. [https://doi.org/10.1890/0012-9658\(2002\)083\[2240:SUAMIH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2240:SUAMIH]2.0.CO;2)
- Nathan R (2008) An emerging movement ecology paradigm. *P Natl Acad Sci USA* 105:19050–19051. <https://doi.org/10.1073/pnas.0808918105>
- Noonan MJ, Martinez-Garcia R, Davis GH et al (2021) Estimating encounter location distributions from animal tracking data. *Methods Ecol Evol* 12:1158–1173. <https://doi.org/10.1111/2041-210X.13597>
- Noser R, Byrne RW (2010) How do wild baboons (*Papio ursinus*) plan their routes? Travel among multiple high-quality food sources with inter-group competition. *Anim Cogn* 13:145–155. <https://doi.org/10.1007/s10071-009-0254-8>
- Palminteri S, Powell GVN, Peres CA (2016) Determinants of spatial behavior of a tropical forest seed predator: the roles of optimal foraging, dietary diversification, and home range defense. *Am J Primatol* 78:523–533. <https://doi.org/10.1002/ajp.22407>
- Pearce F, Carbone C, Cowlishaw G et al (2013) Space-use scaling and home range overlap in primates. *Proc Roy Soc B* 280:20122122. <https://doi.org/10.1098/rspb.2012.2122>
- Potts KB, Chapman CA, Lwanga JS (2009) Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. *J Anim Ecol* 78:1269–1277. <https://doi.org/10.1111/j.1365-2656.2009.01578.x>
- Powell RA (2000) Animal home range and territories and home-range estimators. In: Boitani L, Fuller TK (eds) *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, pp 65–110 <https://www.jstor.org/stable/10.7312/boit11340>
- Robinson JG (1979) Vocal regulation of use of space by groups of titi monkeys *Callicebus moloch*. *Behav Ecol Sociobiol* 5:1–15 <http://www.jstor.org/stable/4599213>
- Roth AM, Cords M (2016) Effects of group size and contest location on the outcome and intensity of intergroup contests in wild blue monkeys. *Anim Behav* 113:49–58. <https://doi.org/10.1016/j.anbehav.2015.11.011>
- Samuel MD, Pierce DJ, Garton EO (1985) Identifying areas of concentrated use within the home range. *J Anim Ecol* 54:711–719. <https://doi.org/10.2307/4373>
- Schick RS, Loarie SR, Colchero F et al (2008) Understanding movement data and movement processes: current and emerging directions. *Ecol Lett* 11:1338–1350. <https://doi.org/10.1111/j.1461-0248.2008.01249.x>
- Seaman DE, Powell RA (1990) Identifying patterns and intensity of home range use. In: Darling LM, Archibald WR (eds) *Bears: their biology and management, A Selection of Papers from the Eighth International Conference on Bear Research and Management*, vol 8. International Association of Bear Research and Management, Victoria, BC, Canada, pp 243–249. <https://doi.org/10.2307/3872925>
- Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: between-group interactions. *Behaviour* 136:595–625. <https://doi.org/10.1163/156853999501487>
- Stolwijk A, Straatman H, Zielhuis G (1999) Studying seasonality by using sine and cosine functions in regression analysis. *J Epidemiol Commun H* 53:235–238. <https://doi.org/10.1136/jech.53.4.235>

- Struhsaker TT (1997) Ecology of an African rain forest. University Press of Florida, Gainesville, FL. <https://doi.org/10.1017/S0266467498240399>
- Struhsaker TT, Leland L (1979) Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv Stud Behav* 9:159–228. [https://doi.org/10.1016/S0065-3454\(08\)60036-4](https://doi.org/10.1016/S0065-3454(08)60036-4)
- Tórrez-Herrera LL, Davis GH, Crofoot MC (2020) Do monkeys avoid areas of home range overlap because they are dangerous? A test of the Risk Hypothesis in white-faced capuchin monkeys (*Cebus capucinus*). *Int J Primatol* 41:246–264. <https://doi.org/10.1007/s10764-019-00110-0>
- Turchin P (1998) Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, MA
- Van Belle S, Porter A, Fernandez-Duque E et al (2018) Ranging behavior and potential for territoriality in equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador. *Am J Phys Anthropol* 167:701–712. <https://doi.org/10.1002/ajpa.23645>
- van de Pol M, Wright J (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim Behav* 77:753–758. <https://doi.org/10.1016/j.anbehav.2008.11.006>
- Van Moorter B, Visscher D, Benhamou S et al (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos* 118:641–652. <https://doi.org/10.1111/j.1600-0706.2008.17003.x>
- Vander Wal E, Rodgers A (2012) An individual-based quantitative approach for delineating core areas of animal space use. *Ecol Modell* 224:48–53. <https://doi.org/10.1016/j.ecolmodel.2011.10.006>
- Waser PM, Wiley RH (1979) Mechanisms and evolution of spacing in animals. In: Marler P, Vandenberg JG (eds) *Handbook of behavioral biology, social behavior and communication*, vol 3. Plenum, New York, pp 159–223
- Wilson ML, Hauser MD, Wrangham RW (2007) Chimpanzees (*Pan troglodytes*) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour* 144:1621–1653. <https://doi.org/10.1163/156853907782512137>
- Wilson ML, Kahlenberg SM, Wells M et al (2012) Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Anim Behav* 83:277–291. <https://doi.org/10.1016/j.anbehav.2011.11.004>
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168. <https://doi.org/10.2307/1938423>
- Wrangham RW, Crofoot MC, Lundy R et al (2007) Use of overlap zones among group-living primates: a test of the risk hypothesis. *Behaviour* 144:1599–1619. <https://doi.org/10.1163/156853907782512092>

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