Behavioral Ecology and Sociobiology (2021) 75:21
https://doi.org/10.1007/s00265-020-02945-7

ORIGINAL ARTICLE

Absentee owners and overlapping home ranges in a territorial species

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Received: 21 September 2020 / Revised: 25 November 2020 / Accepted: 30 November 2020

Abstract

Understanding animals' use of space can shed valuable light on multiple other aspects of behavioral ecology, including social organization, dispersal, and foraging efficiency. Home ranges, territories, core areas, and home range overlaps have been widely studied, but unless animals are directly observed or are tracked remotely on a fine temporal scale, how they actually use the space available to them and how they share (or partition) this space with a community of conspecifics over time cannot be fully understood. Using GPS technology, we tracked three adjacent groups of vervet monkeys (*Chlorocebus pygerythrus*) in Laikipia, Kenya, for 1 year to better understand the processes involved in territoriality and home range overlaps. Home ranges overlapped with any one neighboring group by 12.7–34.7%, but intergroup encounters only occurred in restricted areas within these zones, which defined territorial boundaries. The resources closest to the territorial boundaries were nocturnal core areas with preferred sleeping sites adjacent to short-grass areas offering fewer hiding places for ambush predators and greater visibility for predator detection. Home range overlaps were not neutral zones, the result of shifting home range boundaries over time, or based on intergroup encounters at boundaries, but resulted when groups made incursions beyond their territorial boundaries while the neighbor was far away and likely unaware of the intruders. Thus, territories can be non-exclusive but may still be perceived by the animals themselves as sole-owned, as neighbors only intrude when territory owners are absent from that area.

Significance statement

How animals use their space is a perennial focus in behavioral ecology because space use influences nearly everything else in animals' lives. While tracking has long been used to investigate space use, particularly for nocturnal animals, only direct observation or tracking on a fine scale can reveal the processes involved in the creation or maintenance of home ranges and territories and that cause home range overlaps to persist. We remotely tracked three adjacent groups of vervet monkeys on a fine temporal scale for 1 year. Despite behaving territorially, vervet home ranges overlapped well beyond territorial boundaries because neighbors were "absentee owners," unable to prevent incursions when they were not nearby. Our findings suggest that exclusivity of use in the definition of territoriality may be too strict; animals may behave as if they are exclusive owners even if neighbors' use of space does not reflect it.

Keywords Home range overlaps · Territoriality · Primates · Vervet monkeys · *Chlorocebus pygerythrus* · Kenya

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Communicated by K. Langergraber

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Introduction

Investigation of animal space use has been a persistent interest of behavioral ecologists as a window into understanding individual decisions that affect a broad range of other concerns, including foraging efficiency (Brown 2013, 2014; Potts et al. 2016), predator–prey relationships (Isbell et al. 1990, 2018; Thaker et al. 2011; Ford et al. 2014), dispersal (Waser and Jones 1983; Isbell and Van Vuren 1996; Olupot and Waser 2001), survival and reproduction (Isbell et al. 1993; Strong et al. 2018), social relationships and social organization (Isbell 2004; Lukas and Clutton-Brock 2013; VanderWaal et al. 2014; Willems et al. 2015), and habitat change and conservation (Potts and Lewis 2014; Tucker et al. 2018; Van Cleave et al. 2018). Most animals live in home ranges, often defined as the area an individual uses over time for its normal activities (Burt 1943), and some maintain territories, that part of the home range defended from conspecifics by the owner, presumably because there is some resource, such as food, mates, nesting sites, or sleeping sites worth defending (Burt 1943; Maher and Lott 1995). Within their home ranges, most animals also have core areas, which are used more intensively (Kaufmann 1962). Neighbors often have overlapping home ranges, and sometimes territories and core areas also overlap (Person and Hirth 1991; Cascelli de Azevedo and Murray 2007; Wartmann et al. 2014).

The mapping of home ranges derived from tracking animals within a population on a broad and intermittent temporal scale can help us understand the size of home ranges, the extent of home range overlaps, and locations of core areas (e.g., De Moor and Steffens 1972). However, this approach does not reveal the processes that lead to the development and maintenance of home range overlaps or territoriality and therefore limits our understanding of the functions and significance of different degrees of home range overlap. The processes are possible to know only when neighbors are directly and simultaneously observed and their locations mapped, or they are remotely tracked sufficiently often to identify interactions between neighbors (Maher and Lott 1995). Thus, the processes leading to home range overlap have been highlighted mostly by studies of diurnal animals, such as primates and birds, and more recently, nocturnal mammals fitted with Global Positioning System (GPS) units.

For territorial animals, there are a number of ways in which home range overlap might occur, and mutually exclusive predictions follow from them. Burt (1943) considered areas of home range overlap to be neutral, which predicts tolerance or indifference between neighbors in areas used but not worth defending (Davies and Houston 1981), behavior that might also be expected when home ranges are indefensible and no territories exist. However, interactions between conspecifics in areas of home range overlap may instead be agonistic, and under these social conditions, home range overlap may develop via several alternative pathways. Especially under unstable social or ecological conditions, certain neighbors may push farther into adjacent home ranges by winning agonistic interactions (Cheney and Seyfarth 1987; Isbell et al. 1990). Unless there is a time component to visualizing home ranges, overlaps may then appear to be substantial to investigators, even for animals such as indris (*Indri indri*), who actively defend almost their entire home ranges from conspecifics (Bonadonna et al. 2017, 2020). Home range overlaps that shift over time as a result of competition between neighbors are predicted to be associated both with an asymmetry in resource holding potential (i.e., body size, group size, or number or sex of participants) and the location of encounters moving farther over time into the home range of the losing neighbor. Home range overlaps might also occur as a result of neighbors regularly chasing each other over short distances back and forth across territorial boundaries, as described for Alaotran gentle lemurs (*Hapalemur griseus*) (Nievergelt et al. 1998). In this case, home range overlaps are expected to be minimal and incursions across boundaries are predicted to occur only when both neighbors are present at the boundaries. Finally, extensive home range overlap might occur as a result of animals making repeated incursions past their territorial boundary when the neighbor is too far away to exclude them. This pattern would then appear on home range maps as part of a larger home range for the invader, even though the invader might not intrude when the neighbor is present. In this case, incursions are predicted to occur most often when the neighbor is far away and unaware of the incursions. Home range overlap in blue monkeys (*Cercopithecus mitis*) occurs via this process (Cords 2002; Roth and Cords 2016), but detailed spatio-temporal evidence is lacking.

We examined these predictions in a field study of vervet monkeys (*Chlorocebus pygerythrus*), a territorial primate species widely distributed in eastern to southern Africa that lives in cohesive multi-male, multi-female groups in which both sexes engage in agonistic intergroup encounters and that exhibits variable degrees of home range overlap (Struhsaker 1967a, 1967b; Gartlan and Brain 1968; Henzi and Lucas 1980; Cheney 1981; Isbell et al. 1990; Pasternak et al. 2013). We used GPS technology to map the locations of three contiguous groups of vervets every 15 min for 1 year. The relative movements of these groups enabled us to understand not only the processes establishing home range overlap but also the influence of group size and site occupancy on success in intergroup competition. We also explored resources that vervets potentially perceived as worth defending. In vervets and other species, the involvement of adult females in agonistic intergroup encounters (IGEs) suggests they defend access to food, offspring, or sleeping sites (Wrangham 1980;

Boydston et al. 2001; Payne et al. 2003; Arseneau-Robar et al. 2016). Because most IGEs occurred near sleeping sites, we focused on those sleeping sites and on identifying characteristics that might make the sleeping sites closest to IGEs worth defending.

Methods and materials

Study site and subjects

We conducted a 14-month study from December 2013 to January 2015 in the semiarid bushlands and riverine woodlands around Mpala Research Centre on the Laikipia Plateau in central Kenya (0.29° N, 36.90° E). Mpala is a wildlife conservancy and working cattle ranch with a nearly intact mammalian community; at least 20 species of ungulates and six species of large carnivores inhabit the area (Young et al. 1997; Goheen et al. 2013). Total rainfall in 2014 was 443.2 mm, and as monthly rainfall never exceeded 100 mm, all months were considered dry, with no rainfall seasonality (Herrmann and Mohr 2011; Suire et al. in press). The Ewaso Nyiro River forms the eastern property boundary of Mpala, and tall but patchily distributed *Acacia xanthophloea* trees that provide food and sleeping sites for vervets occur on the river's edges. The home ranges of the three groups of vervets that are the subjects of this study were closely associated with this riverine habitat (Isbell et al. 2018). The groups ranged in size from 15 (BR group: 5 adult females and 3 adult males, based on group counts during re-trapping to remove collars) to 30–35 (HP group: 10–12 adult females and 8–9 adult males, based on near-daily censuses). KU group was intermediate in size (21 individuals, with 6 adult females and 9 adult males, based on opportunistic counts).

Data collection

We used modified box traps (Grobler and Turner 2010) to capture, immobilize, and place collars with GPS units onto seven adult female vervets in the three groups (at least two per group) as females are the philopatric sex. We immobilized them with an intramuscular syringe injection of 10 mg/kg ketamine hydrochloride (Agrar Holland BV, Soest, The Netherlands). Body masses of the captured vervets ranged from 2.7 to 3.9 kg and the GPS collars were 3.6–5.2% of body mass (146–150 g). For additional details, see Isbell et al. (2019). Since vervets live in cohesive groups, we considered the locations of the collared individuals to be representative of the locations of their groups. Collared individuals within each group were located at 47 m ± 69 SD (*n* = 75,368 GPS fixes) from each other, on average.

We programmed all collars to take GPS data every 15 min synchronously throughout the lives of the collars. Each collar transmitted spatial locations until the end of the study or until a collared animal died (range: 2–13 months). We used a base station (e-obs GmbH, Gruenwald, Germany) to download GPS data from each collar remotely when we were within UHF range of the collars. The data are available in Movebank (Wikelski and Kays 2017), an online repository for animal movement data. We obtained estimates of the accuracy of the collars by collecting data from two stationary collars. The mean difference in distance between consecutive readings for these two stationary collars (GPS "noise") was 11 m ± 20 SD (*n* = 275 fixes) and 12 m ± 10 SD (*n* = 847 fixes). The GPS units attempted 303,984 location fixes for all vervets, with an overall success rate of 99.1% (range = 98.0–99.4%).

Data analyses

Sizes of home ranges, core areas, and home range overlaps

Although the collars were programmed to collect locational data synchronously, the time involved in finding sufficient satellites to obtain a given fix could vary among units. Nevertheless, 95% of all fixes occurred within 23 s of the nearest quarter-hour. For data analyses involving the locations of, or proximities between, two collared individuals or two groups, we rounded the true timestamp of each GPS fix to the nearest quarter-hour. If the timestamps of two different GPS fixes for an individual rounded to the same quarter-hour, the fix that was closer in time to the quarter-hour was used and the other fix was discarded.

To find the home range of each vervet group, we first took the GPS data for an entire group and removed relocations that corresponded with duplicated timestamps. In doing so, we created a single and complete group-level track for each group. We then used the "adehabitatHR" package for R (Calenge 2006) to determine each group's utilization distribution (UD) with a kernel density estimation (KDE). The UD is a bivariate function that represents the probability that a given group is found at a particular geographic location. We defined a group's home range as the boundary encompassing 99% of its UD because outliers were rare and reducing to the 95% level excluded infrequent locations that were nonetheless important. In fact, using the 95% level would place IGEs outside home range overlap areas, an impossibility in reality. We defined a group's core area as the boundary encompassing 50% of its UD and further separated the core area into daytime (0630–1845) and nighttime (1900–0615) core areas because limited movement during the night biased unseparated core areas heavily toward sleeping sites. We determined home range overlaps by using the "sp" package for R to find the intersection of adjacent home ranges (Pebesma and Bivand 2005; Bivand et al. 2013).

Resource holding potential and IGE locations

We also calculated daily travel distances (from 0600 hours to 1800 hours) and home range diameters to determine the groups' abilities to defend their home ranges. During calculation of daily travel distances, potential outliers among GPS fixes were flagged if the step length (distance traveled per 15 min) was greater than the 99.9th percentile. We then checked each potential outlier to see if the female was within 200 m of at least one of her collared groupmates. If she was not, the potential outlier was excluded as a confirmed outlier. To control for stochastic variation in GPS fix locations, the vervets had to move 20 m from where they started their day in order for it to contribute to their travel distance. Once they moved beyond 20 m, the same process repeated—they had to move another 20 m from that spot before this distance was added to their daily travel distance. The 20-m cutoff was based on a histogram of the distance between each fix from 2300 to 0300 hours when vervets moved very little, which suggested 20 m would account for most of the GPS "noise," without being too high a threshold that it missed real movement happening at a relatively fine scale (see also Isbell et al. 2017).

A commonly used measure to estimate a group's ability to defend its home range is the defendability (*D*) index, which is based on daily travel distance in relation to home range diameter: groups that travel at least as far as the diameter of the home range in a given day are expected to have defendable home ranges (Mitani and Rodman 1979). The applicability of the *D* index is based on the assumptions that the home range does not exhibit extreme deviation from a circular shape and that all edges of the home range have neighbors. As Mitani and Rodman (1979) pointed out, the *D* index is not appropriate for very oblong ellipses, those with extreme eccentricity. The shapes of the vervet home ranges were highly linear, suggesting that the *D* index is not appropriate to use here. However, because the *D* index is so widely known, we included it. Using the same logic employed by Mitani and Rodman (1979), we also calculated a different index of defendability from the ratio of daily travel distance to home range diameter, as groups must be able to travel far enough in a given day to be able to defend the boundaries of the home range. However, we calculated the diameter as the distance between the northern and southern boundaries of the groups' home ranges. These are the only areas where neighboring groups could be encountered because the habitat is unsuitable for vervets away from the river. Our index leverages the empirical spatial arrangement of vervet home ranges in the region to calculate a more accurate index of defendability. A value of ≥ 1 suggests the home range is defendable because the group can travel at least as far as the two ends of the home range in a given day, whereas a value of < 1 suggests it is not.

We used the R programming language (see Code Availability; R Core Team 2019) to calculate proximities between collared individuals from different groups for each 15-min sample. As a check on its validity, we compared proximities using that method with a matched sample of 2000 proximity values obtained previously with a different method (see Isbell et al. 2018). We found that the current method placed dyads farther apart by 6.9 m ± 2.1 SD (range = 0–14 m), on average, and that greater disparities occurred as inter-individual distances increased, but there was no disparity between methods at proximities within 50 m.

We then extracted all spatial data in which at least one collared individual from one group was within 50 m of a collared individual of another group at a given 15-min sample. These were operationally defined as spatial IGEs that began when at least one collared individual from one group was within 50 m of a collared individual from another group (Oates 1977; Koch et al. 2016a) and ended when the collared individuals from the two groups were no longer within 50 m of each other. Other investigators have used greater distances in defining IGEs (e.g., Cheney 1981; Brown 2014; Ellis and Di Fiore 2019; Van Belle and Estrada 2020), but in those cases, visibility was better or behavioral changes that indicate detection, e.g., intergroup vocalizations, increased vigilance, or displays, were available. Since our study was conducted remotely, we could not use behavior other than relative movements to identify when groups detected each other. Winners and losers of IGEs were defined by the direction of movement of collared individuals as identified by plotting their successive locations by time in Google Earth Pro v. 7.1.5.1557. Winners approached other groups while at the same time losers retreated, and mutual departures in time were scored as "draws," with no winners or losers. Boundaries of intergroup encounter zones (IGEZs) were determined by connecting the four most extreme compass locations of the collared individuals in each group when they were engaged in IGEs. The area within each "box" was considered the IGEZ. These IGEZs defined the territorial boundaries of the groups.

Incursions across territorial boundaries

We also extracted all spatial data when at least one collared individual in a group went beyond the midpoint of its IGEZ. A single event consisted of all consecutive GPS locations, excluding missing data points, during which the group was beyond the midpoint of its IGEZ. We considered such events to be intrusions into the territory of the other group. We calculated mean distances between the intruding group and its neighbor from their proximity at the midpoint in time for each intrusion to determine how close the groups were to each other during incursions.

To investigate relative use of the groups' IGEZs, we calculated for each group the number of days when at least one collared individual was at any time within its group's IGEZ and the neighboring group was elsewhere. The number of days a group spent in its IGEZ on these non-encounter days provided an estimate of land value perceived by that group since its presence there was not constrained at that time by the other group. The group that spent more non-encounter days in its IGEZ compared to its neighbor was interpreted as perceiving that area as having greater value thus being more motivated to defend it (Kitchen et al. 2004; Crofoot et al. 2008; Brown 2013; Markham et al. 2013; Koch et al. 2016b).

Territorial boundaries and defended resources

Because IGEZs were located near nocturnal core areas with major sleeping tree sites (see the "Results" section), we hypothesized that the sleeping sites in those core areas had high perceived value to vervet groups. Since vervets likely use sleeping sites for protection against predators both day and night, at these sites and elsewhere along the river, we measured ecological characteristics thought to be important in reducing the risk of predation (number of trees: Markham et al. 2016; visibility: Cowlishaw 1994; Matsuda et al. 2011; Burger et al. 2020; tree height: Reichard 1998; Wahungu 2001; Bernard et al. 2011; Feilen and Marshall 2014).

We identified sleeping sites based on clusters of GPS locations less than 50 m apart from the same individual vervet within the hours of 18:00–05:45 using Google Earth Pro. We then determined occupancy of sleeping sites by vervet groups for every night when at least one GPS unit was transmitting in a given group. We used the location of the collared group member with the most uninterrupted GPS fixes at 23:00 hours local time in Kenya (UTC + 3) as the location of the group.

Vervets always slept in *A. xanthophloea* trees along the river. After mapping the home ranges and core areas, we counted the number and measured the heights of all 29 *A. xanthophloea* trees that were at least 5 m tall in 6 nocturnal core area sleeping sites, 45 *A. xanthophloea* trees in 11 non-nocturnal core area sleeping sites, and 64 *A. xanthophloea* trees along the river between sleeping sites. To estimate tree heights, we used the ground triangulation method in which an observer standing at least 7 m away from a tree measured the horizontal distance to the tree using a laser rangefinder (Nikon 440 ProStaff Laser Range Finder) and angles from horizontal to the top and base of the tree using a digital clinometer (Peco DCC-1 Digital Compass/Clinometer). We then multiplied the tangent of each of the two angles with the horizontal distance to the tree to obtain an estimate of the tree's height. With these data, we asked if (1) the sleeping sites at the two nocturnal core areas closest to the IGEZs had more or taller *A. xanthophloea* trees than at other sleeping sites, including those at other nocturnal core areas; (2) the groups' nocturnal core area sleeping sites had more or taller trees than trees at sleeping sites outside nocturnal core areas; and (3) *A. xanthophloea* trees in sleeping sites were taller than those outside sleeping sites along the river within the groups' home ranges. We addressed these questions statistically with Mann–Whitney *U* tests, setting statistical significance at $\alpha = 0.05$.

Another quality that may make some sleeping sites preferred over others is the vegetation around them. High-visibility, short-grass habitats occur at our study site along the river where hippopotamus (*Hippopotamus amphibious*) and other grazing mammals suppress woody vegetation and keep the grasses short (McCauley et al. 2018). Short-grass habitats increase visibility and may inhibit predatory behavior by ambush predators such as leopards (*Panthera pardus*) (Sunquist and Sunquist 1989; Bothma et al. 1994; Cowlishaw 1994; FitzGibbon and Lazarus 1995; Bailey 2005; Hill and Weingrill 2007). Some of these short-grass habitats occur near vervet sleeping sites along the river. We classified sleeping sites as occurring either adjacent to "short-grass" areas or to "non-short-grass" areas by visual assessment on site and remotely via Google Earth Pro. We asked if sleeping sites in nocturnal core areas were more often adjacent to short-grass areas than were sleeping sites in other areas and if sleeping sites that were adjacent to short-grass areas were used more often than expected based on their representation among all sleeping sites, which would indicate an active preference of the vervets for sleeping sites with high visibility. These questions were addressed with Fisher's exact probability and χ^2 goodness of fit tests, with statistical significance set at $\alpha = 0.05$.

We mapped home ranges, home range overlaps, core areas, and IGEZs using the "rgdal" package for R (Bivand et al. 2019) and QGIS (QGIS Development Team 2019). As IGEZs of neighboring groups were territorial boundaries that overlapped because of the 50-m operational definition of IGEs, for ease of viewing, we displayed the area encompassing both IGEZs per dyad. We calculated home ranges, home range overlaps, and core areas in hectares with the "sp" package for R (Pebesma and Bivand 2005; Bivand et al. 2013). Statistical tests were conducted with VassarStats (http://vassarstats.net). Because all collared individuals were known and the data were remotely collected on them as focal animals in the field, blind methods were not applicable.

Results

Sizes of home ranges, core areas, and home range overlaps

The population density of vervets was 41.2 individuals per square kilometer within the 172.2 ha that encompassed all three home ranges. This is a minimum estimate because two additional groups that were not monitored likely overlapped to some extent with the northern and southern study groups. Home range size, calculated as 99% UD, was not associated with group size. The largest group, HP, had the smallest home range (26.5 ha), the intermediate-sized group, KU, had the largest home range (59.2 ha), and the smallest group, BR, had a home range intermediate in size between those two (37.3 ha) (Fig. 1). Core area size, calculated as 50% UD, was also not associated with group size. HP group's diurnal core area was the smallest (3.8 ha), KU group's was the largest (11.4 ha), and BR group's was intermediate (7.5 ha). HP group's nocturnal core area was also the smallest (0.4 ha), whereas BR group's was the largest (2.6 ha) and KU group's was intermediate (1.8 ha). HP group and BR group overlapped 28.2% and 34.7% of their home ranges, respectively, with KU group, while KU group overlapped 12.7% of its home range with HP group to the north and 21.9% with BR group to the south. KU group's total home range overlap with its two neighboring groups was 34.6%.

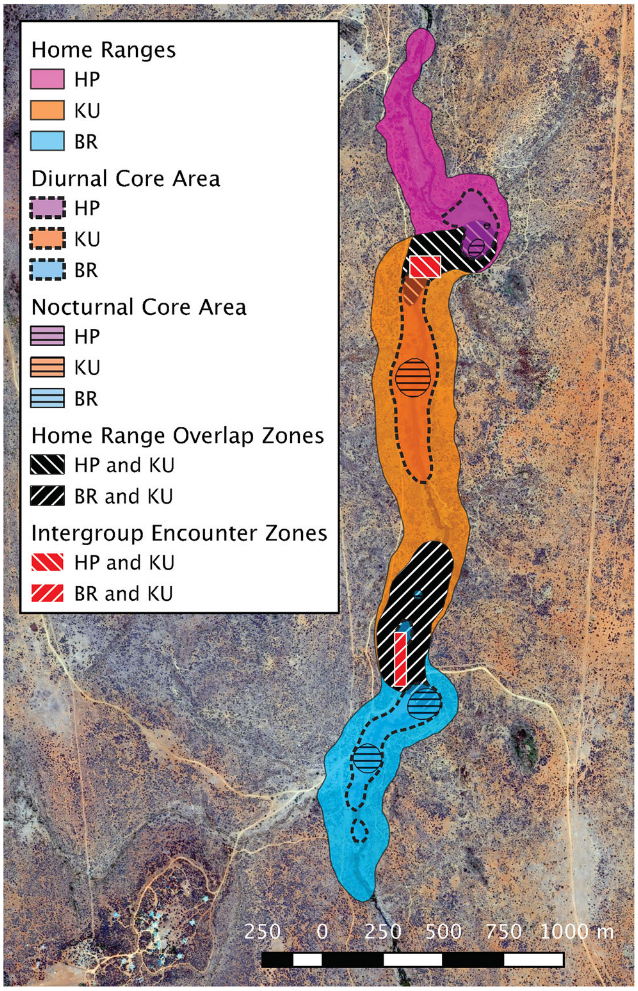

Fig. 1 Home ranges (99% UD), core areas (50% UD), home range overlaps, and intergroup encounter zones of three adjacent vervet groups along the Ewaso Nyiro River, Kenya, from January 2014 to January 2015. Background map: Google Earth Pro

Resource holding potential and IGE locations

Mean daily travel distances across collared females ranged from 1131 m ± 315 SD to 1658 m ± 369 SD. According to the *D* index (Mitani and Rodman 1979), all groups should have been able to defend their ranges: the D index for HP group was 2.0 and 2.3 (each female's score), for KU group, 1.5 and 1.6, and for BR group, 2.2 and 2.4. However, the *D* index may not be appropriate for our study groups given that the groups' home ranges were shaped more like oblong ellipses than circles (Mitani and Rodman 1979). Using the same logic as Mitani and Rodman (1979), we calculated defendability with an alternative index that recognizes only the two ends of a home range as potentially needing to be defended. Thus, if a group can travel the length of its home range in a given day, the home range should be defendable. Ratios of daily travel distance to the north–south home range diameter were 1.0 and 1.2 for HP group females, 1.1 for both BR group females, and 0.7 for both KU group females, suggesting that KU group could not defend its longer home range.

Across the entire study, KU group had only 10 IGEs with HP group and only seven with BR group. One to four IGEs per month were spread across 7 months, from March to September. They began at various times of the day, ranging from 0830 to 1645, but the peak hours were from 10:00–12:00 when seven of the 17 IGEs occurred. During IGEs, groups engaged for less than 15 min up to 75 min. No groups were tolerant of, or indifferent to, their neighbors when in proximity. If they were tolerant of, or indifferent to, their neighbors, we would expect a variety of movement patterns between groups and long durations within proximity. All movements between groups were consistent, however, and consistent with observed IGEs in other vervet populations (LAI, pers. obs.). All IGEs between KU group and HP group were draws and consisted of mutual approaches, with the larger HP group coming from the north near its nocturnal core area and KU group coming from the south, followed by lack of movement before the groups mutually retreated. They spent an average of 28.5 min (± 19.3 SD) in proximity during their IGEs. The shortest (≤ 15 min) IGEs were also the most frequent (5 of 10 IGEs), and only one lasted as long as 75 min. All IGEs between KU group and BR group were won by BR, the smaller group. BR group always approached KU group from the south near its largest nocturnal core area, followed by KU group retreating back north (Fig. 2). Thus, in no interactions did the larger group win. During their IGEs, they were in proximity an average of 32.1 min (± 29.3 SD), with two IGEs extending to 75 min. All others lasted ≤ 15 min.

Relative numbers of adult males in groups also did not clearly influence encounter outcomes. While the draws between HP group and KU group could have been related to their having had similar numbers of adult males, BR group won all its IGEs with KU group despite having 67% fewer

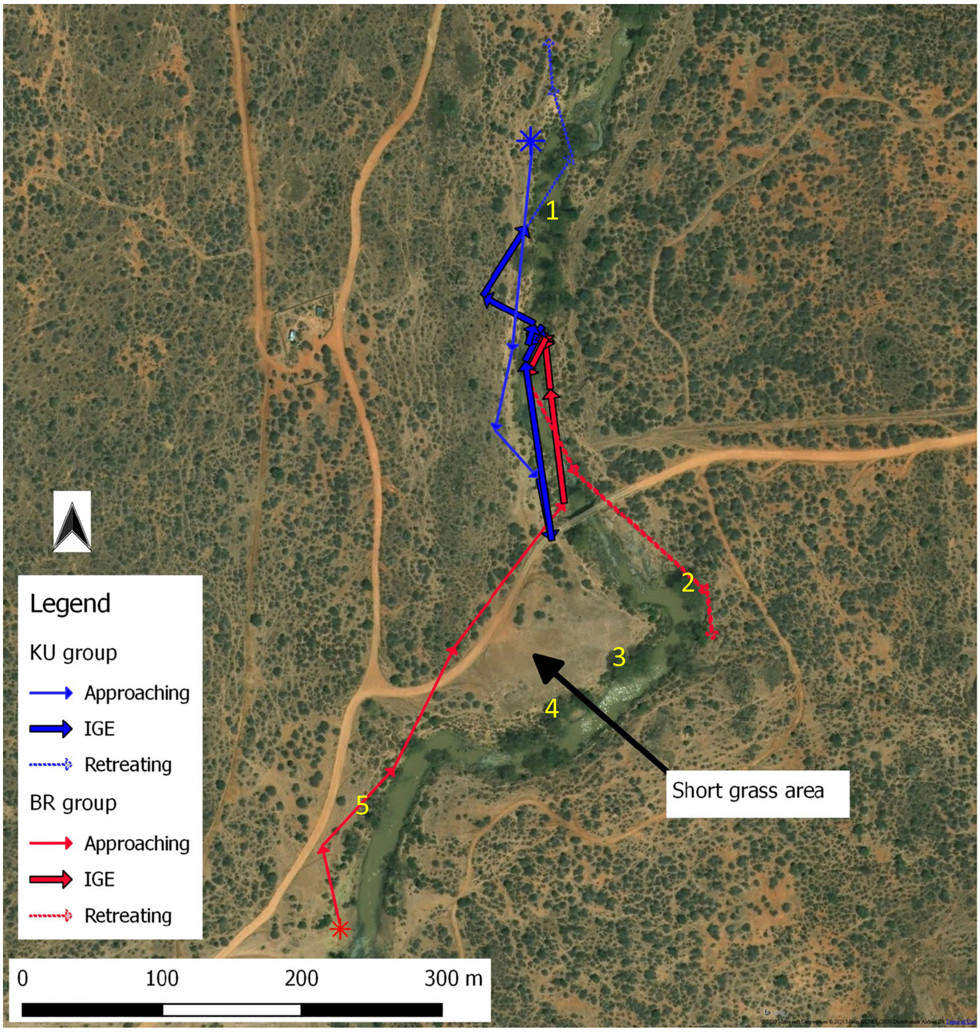

Fig. 2 Example of an intergroup encounter (IGE) between KU group (blue line) and BR group (red line). Lines represent paths taken by the groups in the hour before the IGE, beginning with a star symbol, until the hour after the IGE. Arrow tips indicate GPS locations of a collared individual at 15-min intervals. Thicker lines indicate the IGE itself, when collared individuals were within 50 m of each other. Sleeping sites identified by numbers: 1 = Island South, 2 = OJ Bridge (in nocturnal core area), 3 = Bridge (in nocturnal core area), 4 = Bridge South (in nocturnal core area), 5 = Bridge Rd. Note the large short-grass area in BR group's home range, adjacent to core area sleeping sites. Background map: Google Earth Pro

adult males. Similarly, relative numbers of adult females did not influence encounter outcomes. HP group had twice the number of adult females that KU group had, but all IGEs resulted in draws, and BR group had one fewer adult female than KU group but won all its IGEs with KU group. Finally, all IGEs during the year occurred within a small (1.1 ha) region of the home ranges of the groups (Fig. 1). These results are not consistent with home range overlaps occurring as a result of larger groups winning IGEs and then encroaching farther over time into the losing groups' home ranges.

Relationships between groups were instead mirrored by group differences in land use. Greater asymmetry in IGE outcomes was associated with similar asymmetry between groups in the number of days they spent in their IGEZs. While KU group spent fewer days in each of its northern and southern IGEZs (106 of 354 days and 40 of 367 days, respectively, when KU and each of its neighbors had functioning collars) than either of its neighbors (HP group: 152 of 354 days; $\chi^2 = 12.9$, $p = 0.0003$; BR group: 178 of 367 days; $\chi^2 = 124.26$, $p < 0.0001$), the asymmetry in IGEZ use was greater between KU group and BR group (10.9% vs 48.5% of all days) than between KU group and HP group (29.9% vs 42.9% of all days). The outcome of competitive interactions based on site occupancy is consistent with the concept of perceived land ownership and territoriality.

Incursions across territorial boundaries

In going past its IGEZ (i.e., its defended territorial boundary), HP group extended into KU group's diurnal core area but not into its more centrally located nocturnal core area. BR group did not breach KU group's diurnal or nocturnal core areas, but it did establish two small core areas that were well within KU group's home range, in line with data that suggest KU group's home range was not defendable. However, although HP and BR groups had defendable home ranges, KU group nonetheless breached both HP group's diurnal and nocturnal core areas as well as BR group's diurnal core area and its largest nocturnal core area (Fig. 1).

Intrusions into neighbors' territories occurred most often when the neighboring group was not nearby. When HP group made incursions past its territorial boundary into KU group's territory, KU group was, on average, 724 m ± 410 SD farther south. Only one of its 76 incursions (1.3%) included an IGE. When BR Group made incursions past its territorial boundary into KU group's territory, KU group was, on average, 801 m ± 386 SD farther north. Only five of its 127 (3.9%) incursions included IGEs. KU group's incursions past its territorial boundary into HP group's territory were made when HP Group was, on average, 301 m ± 166 SD farther north. Only six of its 127 (4.7%) incursions developed into IGEs. Finally, KU group's incursions past its territorial boundary and into BR group's territory were made when BR group was, on average, 398 m ± 208 SD farther south. Only two of its 31 (6.4%) incursions included IGEs. Table 1 provides a summary of our findings thus far for each group.

Territorial boundaries and defended resources

As all IGEs were close to nocturnal core areas, we examined sleeping site use and characteristics. Different vervet groups sometimes used the same sleeping sites but never on the same night. Of HP group's two nocturnal core areas, the larger one included the group's main sleeping site, which the group used on 81% (290 of 358) of all nights and which was closest to HP group's territorial boundary (Table 2; Fig. 1). BR group's largest and most frequently used nocturnal core area was also closest in proximity to BR group's territorial boundary with KU group. It included three sleeping sites where the group slept on 42% (58 of 378) of all nights (Table 2; Fig. 1). KU group had just one nocturnal core area with one sleeping site, where the group slept on 67% (245 of 367) of all nights (Table 2; Fig. 1). KU group's nocturnal core area was located in the center of its home range, far from either of its territorial boundaries (Fig. 1).

We did not detect a significant difference in the number of *A. xanthophloea* trees per sleeping site or their height at the sleeping sites in the two nocturnal core areas nearest the territorial boundaries compared to trees at other sleeping sites in and outside other nocturnal core areas (number per sleeping sites in two core areas nearest boundaries: mean ± SD = 5.8 ± 4.0, median = 6.5; number at other sleeping sites: mean ± SD = 4.2 ± 2.7, median = 5.0; $U = 30.5$, $n_1 = 12$, $n_2 = 4$, $p > 0.5$, two-tailed; height at sleeping site in two core areas nearest boundaries: mean ± SD = 17.3 ± 3.4 m, median = 16.8 m; height at other sleeping sites: mean ± SD = 17.9 ± 4.7 m, median = 17.4 m; Mann–Whitney *U* test, $U = 524.5$,

Table 1 Summary of relevant characteristics of three vervet groups studied near Mpala Research Centre, Kenya, from January 2014–January 2015 using GPS technology deployed on 1–3 adult females per group. KU group's home range was located between HP group's to the north and BR group's to the south

Vervet group			
Characteristic	HP	KU	BR
Group size	30–35	21	15
Number of adult males	8–9	9	3
Number of adult females	10–12	6	5
Home range size (ha)	26.5	59.2	37.3
Diurnal core area size (ha)	3.8	11.4	7.5
Nocturnal core area size (ha)	0.4	1.8	2.6
Home range overlap (%)	28.2	HP: 12.7 BR: 21.9	34.7
Mean daily travel distance (m)	1131–1337	1350–1402	1547–1658
D index	2.0 and 2.3	1.5 and 1.6	2.2 and 2.4
Alternative *D* index	1.0 and 1.2	0.7	1.1
Number of incursions into neighbor's territory	76	HP: 127 BR: 31	127
Number of IGEs	10	HP: 10 BR: 7	7
IGE outcome	All draws	HP: all draws BR: all lost	All won
Days in IGEZ (%)	42.9	Northern IGEZ: 29.9 Southern IGEZ: 10.9	48.5
Neighbor's mean proximity during incursions (m)	724	HP: 301 BR: 398	801
Incursions with IGEs (%)	1.3	HP: 4.8 BR: 6.4	3.9

IGE intergroup encounter, *IGEZ* intergroup encounter zone

Table 2 Numbers of nights occupied at sleeping sites (ordered here from north to south) by three groups of vervets studied near Mpala Research Centre, Kenya, from January 2014 to January 2015 using GPS technology deployed on 1–3 adult females per group

Sleeping site	HP group	KU group	BR group
Pump	6		
Pre-Pump	1		
Canal	2		
HP Canal	5		
HP Weir	2[a]		
OJ Hippo Pool	8		
HP Croc Corner	3[a]		
HP Songmeter	40[a, b]		
Hippo Pool	290[a, b, c]	1[a, c]	
OJ HP River	1		
Pre-HP		10	
OJ Johanna North		6	
Johanna North		245[a, b]	
OJ Johanna Main		20	
Johanna		24[a]	
Johanna South		23[a]	
River Glade		1[a]	
Island North		3	2
Island		30	49[b]
Island South[1]		4	16
OJ Bridge[2]			103[b, c]
Bridge[3]			51[a, b, c]
Bridge South[4]			4[a, b, c]
Bridge Rd.[5]			4[a]
Bridge Exclosure			120[a, b]
Center Pump			1
Camp Rd.			26
South Camp Rd.			2
Total	358	367	378

Superscripts 1–5: sleeping sites identified in Fig. 2

[a] Sleeping sites adjacent to short-grass areas

[b] Nocturnal core area sleeping sites

[c] In core areas nearest intergroup encounter zones (IGEZs)

$z = 0.72$, $n_1 = 51$, $n_2 = 23$, $p = 0.47$, two-tailed). Similarly, we did not detect a significant difference in the numbers or heights of *A. xanthophloea* trees at core area sleeping sites compared to non-core area sleeping sites (number in core areas: mean ± SD = 4.8 ± 3.6, median = 4.5; number in non-core areas: mean ± SD = 4.1 ± 2.8, median = 5.0; $U = 36.5$, $z = -0.3$, $n_1 = 11$, $n_2 = 6$, $p = 0.76$, two-tailed; height in core areas: mean ± SD = 17.1 ± 4.2 m, median = 16.8 m; height in non-core areas: mean ± SD = 18.2 ± 4.4 m, median = 17.8 m; $U = 562$, $z = 1.0$, $n_1 = 45$, $n_2 = 29$, $p = 0.32$, two-tailed). Finally, we did not detect a significant difference in the heights of *A. xanthophloea* trees at sleeping sites compared to those outside sleeping sites within the home ranges of the three groups (inside sleeping sites: mean ± SD = 17.8 ± 4.3 m, median = 17.2 m; outside sleeping sites: mean ± SD = 17.1 ± 4.7 m, median = 16.7 m; $U = 2020.5$, $z = 1.48$, $n_1 = 74$, $n_2 = 64$, $p = 0.14$, two-tailed).

Collectively, nocturnal core area sleeping sites were more likely (6/8 = 75%) than non-core area sleeping sites (6/20 = 30%) to be adjacent to short-grass areas (Fisher's exact probability test: $p = 0.04$, two-tailed), and this result was consistent across groups (Fig. 3). HP group slept in trees adjacent to short-grass areas on 335 of 358 (93.6%) nights, KU group, on 294 of 367 (80.1%) nights, and BR, on 179 of 378 (47.4%) nights. All groups slept next to short-grass habitats on more nights than expected based on their representation among all sleeping sites (HP group: $\chi^2 = 425.93$, df = 1, $p < 0.0001$; KU group: $\chi^2 = 176.42$, df = 1, $p < 0.0001$; BR group: $\chi^2 = 19.22$, df = 1, $p < 0.0001$).

Discussion

Our study presents a complete record of all intergroup encounters that occurred to within 50 m for three groups of vervet monkeys over 1 year's time, obtained via the deployment of GPS collars that recorded the locations of 1–3 adult females in each group every 15 min throughout the diel period. All IGEs occurred only at highly restricted locations within the home ranges (Fig. 1). During IGEs, groups moved in ways that did not suggest indifference or tolerance but that indicated agonistic interactions, i.e., one group moved toward the neighbor and the neighbor retreated, or both groups moved toward each other and then both retreated. These results suggest that at our study site, as elsewhere, vervets are territorial, a rarity among primate species that live in multi-male, multi-female groups (Isbell et al. 2002). Moreover, both indices of defendability largely confirm that the home ranges were defendable.

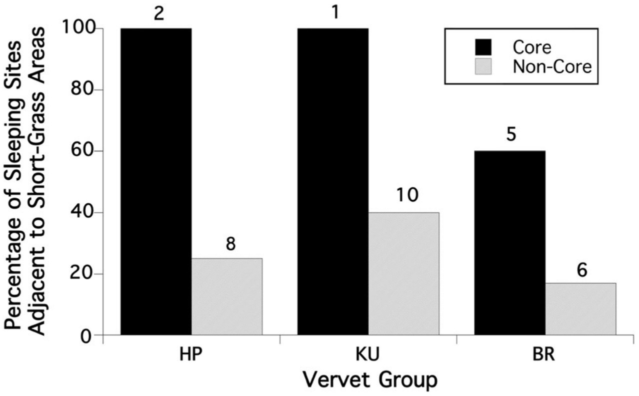

Fig. 3 Percentage of each vervet group's nocturnal core and non-core sleeping sites adjacent to short-grass areas. Numbers above the bars are sample sizes

The concept of territoriality has a long history. Some authors have viewed territories as fixed areas that are exclusively used. If exclusivity could not be achieved, it was not considered a territory (Pitelka 1959; Schoener 1968; Brown and Orians 1970; Börger et al. 2008; Asencio et al. 2018). Others, however, have viewed territories as also requiring defense via, for example, scent, vocalizations, or aggression (e.g., Gibb 1956; Jarman 1974; see Maher and Lott (1995) for discussion). We found the territorial boundaries to be fixed but well within areas of home range overlaps, which challenges the exclusive use component of territoriality in that part of the groups' home ranges. In the "Introduction" section, we presented ways in which home range overlap can be established: (1) neutral areas, (2) shifting boundaries over time as larger groups displace smaller groups, (3) small intrusions only during active engagement at territorial boundaries, and (4) larger incursions when the neighbors are not present. Of those four scenarios, we found support for the last one.

Had we not documented the locations and outcomes of IGEs but simply plotted the locations of the groups on a map, the areas where the groups no longer overlapped would have been interpreted as their territorial boundaries. This approach would have left large gaps between the territorial boundaries of adjacent groups that could be interpreted erroneously as neutral areas. Each group had exclusive use of some of their home ranges but exclusivity occurred well short of their actual, defended territorial boundaries. Exclusivity occurred not because the owners kept neighbors from encroaching but because neighboring groups stopped moving forward in the absence of the owners.

In our study, vervet groups often could not prevent intrusions beyond territorial boundaries simply because they were not always nearby. Groups nonetheless behaved as if they were territorial, i.e., visualization of the movement data revealed that groups defended a fixed area whenever they and the neighboring group were within 50 m of each other. Moreover, the outcomes of IGEs closely followed a common rule of territory ownership in that group size had no effect but the group spending more time at the location of IGEs was more likely to win (site-specific dominance) (Kaufmann 1983; Maher and Lott 1995). Territoriality in our study population of vervets appears to be best aligned with the definition of territoriality proposed by Maher and Lott (1995, p. 1589): "a fixed space from which an individual, or group of mutually tolerant individuals, actively excludes competitors for a specific resource or resources," although with the caveat that active exclusion does not always mean effective exclusion.

All IGEs occurred near two nocturnal core areas, and the directions from which the groups with those core areas approached their neighbor during IGEs suggest that they were attempting to prevent the neighbors' access to those core areas. Unlike olive baboons (*Papio anubis*) at the same study site (Bidner et al. 2018), vervets never shared sleeping sites with another group on the same night nor has sharing been seen at other vervet study sites (Amboseli and Segera, Kenya: LAI, pers. obs.; Burman Bush and Samara, South Africa: S.P. Henzi, pers. comm.).

The nocturnal core areas closest to the territorial boundaries included sleeping sites near short-grass habitats. Short-grass areas are similar to burned areas; reduced vegetation height makes animals safer from ambush predators because visibility is good and there are fewer places for ambush predators to hide (Jaffe and Isbell 2009; Herzog et al. 2016; Hoare 2019). We suggest that vervets valued and competed for these particular sleeping sites because their enhanced visibility made it easier for vervets to detect predators while going to the trees in the evenings and leaving the trees in the mornings and for as long as they were in the area during the daytime. Competition for sleeping sites has also been suggested for Milne-Edwards' sportive lemur (*Lepilemur edwardsi*: Rasoloharijaona et al. 2003), golden brown mouse lemurs (*Microcebus ravelobensis*: Braune et al. 2005) and pig-tailed macaques (*Macaca leonina*; José-Domínguez et al. 2015), and cavity-nesting birds (Lindell 1996) such as green woodhoopoes (*Phoeniculus purpureus*) (Radford and du Plessis 2004).

Meta-analyses within and among species of primates suggest that larger home ranges have larger overlaps, which is thought to reflect the economics of defensibility: groups with larger home ranges have more difficulty detecting intruders (Pearce et al. 2013). Our study supports this hypothesis. The two groups with smaller home ranges expanded into the largest home range to a greater extent than the group with the largest home range expanded into its neighbors' home ranges. It is unclear why groups did not encroach farther than they did, given that their neighbors were so often absent during incursions. They may perceive a greater risk of predation as they move farther into less familiar areas (Isbell et al. 1990). Alternatively, they may not always know the location of their neighbor, and as they move farther into the neighbor's home range, they become statistically more likely to encounter that group. Such an encounter may be costly especially if territory ownership is the best predictor of encounter outcome.

Interpretations of land use, home range overlaps, and behavior in primates vary considerably. Territorial animals are often considered to have little, if any, home range overlap (Sekulic 1982; van Schaik et al. 1992; Nievergelt et al. 1998; Gursky 2007; Potts and Lewis 2014), which is consistent with the view that minimal home range overlap indicates low tolerance between neighbors (Wrangham et al. 2007). Indeed, Willems et al. (2013) assumed that extensive home range overlap occurs only in the absence of territoriality. The perspective that territorial primates have little home range overlap may have been influenced by earlier studies of small non-primate mammals, such as rodents, many of which do not live in social groups. Larger-bodied mammals have greater home range overlap than smaller-bodied animals do (Jetz et al. 2004), and animals that live in groups have larger home ranges than solitary animals do, all else being equal (McNab 1963; Schoener 1968; Milton and May 1976; Clutton-Brock and Harvey 1977), making their home ranges more difficult to defend completely (see also Wolff 1993). Among non-primates, for instance, territorial Ethiopian wolf packs (*Canis simensis*) had home range overlaps of 19–41% (Tallents et al. 2012), and territorial African wild dog packs (*Lycaon pictus*) had home range overlaps of up to 62% (Jackson et al. 2017; Jordan et al. 2017). The vervet groups in our population had home range overlaps of 12.7–34.6% with adjacent groups. Similarly, territorial, socially monogamous owl monkeys (*Aotus azarae*) had home range overlaps of 41–56% with other groups (Wartmann et al. 2014); territorial mixed-species groups of saddleback and mustached tamarins (*Saguinus fuscicollis* and *S. mystax)*, 76% (Peres 1992); and territorial Verreaux's sifakas (*Propithecus verreauxi*), 36–64% (Benadi et al. 2008). Home range overlaps in sifakas were interpreted as areas in which neighboring groups do not exclude each other (Benadi et al. 2008), which is consistent with Burt's (1943) description of home range overlap as a neutral zone.

In some primate species with agonistic intergroup relationships, overlap areas are underused (e.g., chimpanzees (*Pan troglodytes*), red-tailed monkeys (*C. ascanius*), and white-faced capuchins (*Cebus capucinus*): Wrangham et al. 2007; Phayre's leaf monkeys (*Trachypithecus phayrei*): Gibson and Koenig 2012; female spider monkeys (*Ateles geoffroyi*: Chapman 1990). In other species, overlap areas are not avoided (e.g., red howler monkeys (*Alouatta seniculus*): Sekulic 1982; bald-faced saki monkeys (*Pithecia irrorata*): Palminteri and Peres 2012, Palminteri et al. 2016; saddleback and mustached tamarins: Peres 1992; Verreaux's sifakas: Benadi et al. 2008). In our study, the existence of core areas within overlap areas indicates that the groups did not underuse their overlap areas. Wrangham et al. (2007) hypothesized that underuse of overlap areas occurs when the risk of lethal interactions is high, which they termed the risk hypothesis. Related to this hypothesis, Stamps and Krishnan (2001) suggested that the extent of home range overlap depends on the strength of punishment that neighbors are willing to inflict on each other, with those engaging in escalated fights, for example, having mutually exclusive home ranges and those engaging in little punishment having highly overlapping home ranges. We add that when owners are not often nearby to engage in fights, the risk of strong punishment is also reduced. Female transfer between groups is associated with low aggression and extensive home range overlap in catarrhine primates (Isbell and Van Vuren 1996), but relative use of overlap and non-overlap areas might also be informative in estimating the strength of intergroup punishment. In vervets, occasional transfer of adult females to other groups (Cheney 1987; Isbell et al. 1990), lack of avoidance of overlap areas, and absentee owners suggest that the risk of strong punishment is fairly low. Low risk of strong punishment might help to explain their substantial home range overlap even while being territorial. Consistent with the view that extent of home range overlap is related to the intensity of punishment, home range overlap among vervet groups at Samara is greater than that reported for any other vervet population, and when groups meet, their interactions are not invariably agonistic (Pasternak et al. 2013).

In our study, we operationally defined "home range" as the boundary encompassing 99% of a group's utilization distribution (UD). While this definition is fairly common, it may not necessarily reflect the animals' perception of what is and what is not theirs. In the future, investigating behavior such as vigilance as groups move farther into the overlap area away from the territorial boundary might be fruitful. If they spend increasingly more time vigilant as they move farther from their territorial boundary, it might suggest that they perceive the land as belonging less to them than to the other group, even though home range maps would show it as their land, too.

Acknowledgments We thank G. Omondi and M. Mutinda for their veterinary services during the capture process; W. Longor, A. Sneath, K. VanderWaal, and J. Wanjala for additional field assistance; and M. Kinnaird and the staff at Mpala Research Centre for logistical assistance. We also thank associate editor Kevin Langergraber and two anonymous reviewers for their constructive comments and suggestions on an earlier version.

Funding This research was supported by the National Science Foundation (Grant Nos. BCS 99-03949 and BCS 1266389), the Leakey Foundation, and the University of California, Davis, Committee on Research to LAI; Wenner-Gren Foundation (Grant No. 8386) to LRB, and an NSF Graduate Research Fellowship and a UC Davis Dean's Distinguished Graduate Fellowship to JCL.

Data availability The data used for this study are available at Movebank.org or from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethics approval This study was approved by the University of California, Davis, under IACUC protocol # 17477, and the Government of Kenya (NACOSTI permit # P/15/5820/4650). Permission to conduct research in Kenya was granted by NACOSTI (permit # P/15/5820/4650), and the Kenya Wildlife Service provided local affiliation. All applicable international, national, and institutional guidelines for the use of animals were followed. The study also conformed to the International Primatological Society's and American Society of Primatologists' Code of Best Practices for Field Primatology.

Consent to participate Not applicable

Consent for publication Not applicable

Code availability Openly available at https://github.com/CarterLoftus/Isbell_et_al_Absentee_Owners. DOI: https://doi.org/10.5281/zenodo.4015395

References

Arseneau-Robar TJM, Taucher AL, Müller E, van Schaik C, Bshary R, Willems EP (2016) Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. Proc R Soc B 283:20161817

Asencio N, José-Domínguez JM, Dunn JC (2018) Socioecological factors affecting range defensibility among howler monkeys. Int J Primatol 39:90–104

Bailey TN (2005) The African leopard: ecology and behavior of a solitary felid. The Blackburn Press, Caldwell

Benadi G, Fichtel C, Kappeler P (2008) Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). Am J Primatol 70:956–965

Bernard H, Matsuda I, Hanya G, Ahmad AB (2011) Characteristics of night sleeping trees of proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. Int J Primatol 32:259–267

Bidner LR, Matsumoto-Oda A, Isbell LA (2018) The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. Am J Primatol 80:e22932

Bivand R, Keitt T, Rowlingson B (2019) rgdal: bindings for the 'Geospatial' data abstraction library. R package version 1.4-8, https://CRAN.R-project.org/package=rgdal. Accessed 15 May 2020

Bivand RS, Pebesma EJ, Gomez-Rubio V (2013) Applied spatial data analysis with R, 2nd edn. Springer, New York. https://www.asdar-book.org/. Accessed 15 May 2020

Bonadonna G, Torti V, SorrentinoV RRM, Zaccagno M, Gamba M, Tan CL, Giacoma C (2017) Territory exclusivity and intergroup encounters in the indris (Mammalia: Primates: Indridae: *Indri indri*) upon methodological tuning. Eur Zool J 84:238–251

Bonadonna G, Zaccagno M, Torti V, Valente D, De Gregoiro C, Randrianarison RM, Tan C, Gamba M, Giacoma C (2020) Intra- and intergroup spatial dynamics of a pair-living singing primate, *Indri indri*: a multiannual study of three indri groups in Maromizaha Forest, Madagascar. Int J Primatol 41:224–245

Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol Lett 11:637–650

Bothma JP, van Rooyen N, Theron GK, leRiche EAN (1994) Quantifying woody plants as hunting cover for southern Kalahari leopards. J Arid Environ 26:273–280

Boydston EE, Morelli TL, Holecamp KE (2001) Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). Ethology 107:369–385

Braune P, Schmidt S, Zimmerman E (2005) Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. Behav Ecol Sociobiol 58:587–596

Brown JL, Orians GH (1970) Spacing patterns in mobile animals. Annu Rev Ecol Syst 1:346–352

Brown M (2013) Food and range defense in group-living primates. Anim Behav 85:807–816

Brown M (2014) Patch occupation time predicts responses by grey-cheeked mangabeys (*Lophocebus albigena*) to real and simulated neighboring groups. Int J Primatol 35:491–508

Burger AL, Fennessy J, Fennessy S, Dierkes PW (2020) Nightly selection of resting sites and group behavior reveal antipredator strategies in giraffe. Ecol Evol 10:2917–2927

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Cascelli de Azevedo FC, Murray DL (2007) Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. Biol Conserv 137:391–402

Chapman CA (1990) Association patterns of spider monkeys: the influence of ecology and sex on social organization. Behav Ecol Sociobiol 26:409–414

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatol 35:124–146

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 267–281

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behav Ecol Sociobiol 21:375–386

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. J Zool (Lond) 183:1–39

Cords M (2002) Friendship among adult female blue monkeys (*Cercopithecus mitis*). Behaviour 139:291–314

Cowlishaw G (1994) Vulnerability to predation in baboon populations. Behaviour 131:293–304

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. P Natl Acad Sci USA 105:577–581

Davies NB, Houston AI (1981) Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. J Anim Ecol 50:157–180

De Moor PP, Steffens FE (1972) The movements of vervet monkeys (*Cercopithecus aethiops*) within their ranges as revealed by radio-tracking. J Anim Ecol 41:677–687

Ellis K, Di Fiore A (2019) Variation in space use and social cohesion within and between four groups of woolly monkeys (*Lagothrix lagotricha poeppigii*) in relation to fruit availability and mating opportunities at the Tiputini Biodiversity Station, Ecuador. In: Reyna-Hurtado R, Chapman CA (eds) Movement ecology of neotropical forest mammals. Springer Switzerland, Cham, pp 141–171

Feilen KL, Marshall AJ (2014) Sleeping site selection by proboscis monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia. Am J Primatol 76:1127–1139

FitzGibbon CD, Lazarus J (1995) Antipredator behavior of Serengeti ungulates: individual differences and population consequences. In: Sinclair ARE, Arcese P (eds) Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, pp 274–296

Ford AT, Goheen JR, Otieno TO, Bidner L, Isbell LA, Palmer TM, Ward D, Woodroffe R, Pringle RM (2014) Large carnivores make savanna tree communities less thorny. Science 346:346–349

Gartlan JS, Brain CK (1968) Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. In: Jay PC (ed) Primates: studies in adaptation and variability. Holt, Rhinehart and Winston, New York, pp 253–292

Gibb J (1956) Food, feeding habits and territory of the rock pipit *Anthrus spinoletta*. Ibis 98:506–530

Gibson L, Koenig A (2012) Neighboring groups and habitat edges modulate range use in Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). Behav Ecol Sociobiol 66:633–643

Goheen JR, Palmer TM, Charles GK, Helgen KM, Kinyua SN, Maclean JE, Turner BL, Young HS, Pringle RM (2013) Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. PLoS One 8:e55192

Grobler JP, Turner TR (2010) A novel trap design for the capture and sedation of vervet monkeys (*Chlorocebus aethiops*). S Afr J Wildl Res 40:163–168

Gursky SL (2007) The spectral tarsier. Pearson Prentice Hall, Upper Saddle River

Henzi SP, Lucas JW (1980) Observations on the inter-troop movement of adult vervet monkeys (*Cercopithecus aethiops*). Folia Primatol 33: 220–235

Herrmann S, Mohr KI (2011) A continental-scale classification of rainfall seasonality regimes in Africa based on gridded precipitation and land surface temperature products. J Appl Meteorol Climatol 50: 2504–2513

Herzog NM, Keefe ER, Parker CH, Hawkes K (2016) What's burning got to do with it? Primate foraging opportunities in fire-modified landscapes. Am J Phys Anthropol 159:432–441

Hill RA, Weingrill T (2007) Predation risk and habitat use in chacma baboons (*Papio hamadryas ursinus*). In: Gursky S, Nekaris KAI (eds) Primate anti-predator strategies. Springer, New York, pp 339–354

Hoare S (2019) The possible role of predator-prey dynamics as an influence of early hominin use of burned landscapes. Evol Anthropol 28: 295–302

Isbell LA (2004) Is there no place like home? Ecological bases of dispersal in primates and their consequences for the formation of kin groups. In: Chapais B, Berman C (eds) Kinship and behavior in primates. Oxford University Press, New York, pp 71–108

Isbell LA, Bidner LR, Crofoot MC, Matsumoto-Oda A, Farine DR (2017) GPS-identified, low-level nocturnal activity of vervets (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*) in Laikipia, Kenya. Am J Phys Anthropol 164:203–211

Isbell LA, Bidner LR, Omondi G, Mutinda M, Matsumoto-Oda A (2019) Capture, immobilization, and Global Positioning System collaring of olive baboons (*Papio anubis*) and vervets (*Chlorocebus pygerythrus*): lessons learned and suggested best practices. Am J Primatol 81:e22997

Isbell LA, Bidner LR, Van Cleave EK, Matsumoto-Oda A, Crofoot MC (2018) GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. J Hum Evol 118:1–13

Isbell LA, Cheney DL, Seyfarth RM (1990) Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Behav Ecol Sociobiol 27:351–358

Isbell LA, Cheney DL, Seyfarth RM (1993) Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? Anim Beahv 45:729–734

Isbell LA, Cheney DL, Seyfarth RM (2002) Why vervet monkeys (*Cercopithecus aethiops*) live in multimale groups. In: Glenn M, Cords M (eds) The guenons: diversity and adaptation in African monkeys. Kluwer Academic/Plenum Publishers, New York, pp 173–187

Isbell LA, Van Vuren D (1996) Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour 133:1–36

Jackson CR, Groom RJ, Jordan NR, McNutt JW (2017) The effect of relatedness and pack size on territory overlap in African wild dogs. Mov Ecol 5:10

Jaffe KE, Isbell LA (2009) After the fire: benefits of reduced ground cover for vervet monkeys (*Cercopithecus aethiops*). Am J Primatol 71:252–260

Jarman PJ (1974) The social organisation of antelope in relation to their ecology. Behaviour 48:215–266

Jetz W, Carone C, Fulford J, Brown JH (2004) The scaling of animal space use. Science 306:266–268

Jordan NR, Buse C, Wilson AM, Golabek KA, Apps PJ, Lowe JC, Van der Weyde LK, McNutt JW (2017) Dynamics of direct inter-pack encounters in endangered African wild dogs. Behav Ecol Sociobiol 71:115

José-Domínguez JM, Asensio N, García García CJ, Huynen M-C, Savini T (2015) Exploring the multiple functions of sleeping sites in northern pig-tailed macaques (*Macaca leonina*). Int J Primatol 36:948–966

Kaufmann JH (1962) Ecology and social behavior of the coati, *Nasua nirica* on Barro Colorado Island Panama. Univ Calif Publ Zool 60: 95–222

Kaufmann JH (1983) On the definitions and functions of dominance and territoriality. Biol Rev 58:1–20

Kitchen DM, Cheney DL, Seyfarth RM (2004) Factors mediating intergroup encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197–218

Koch F, Signer J, Kappeler PM, Fichtel C (2016a) Intergroup encounters in Verreaux's sifakas (*Propithecus verreauxi*): who fights and why? Behav Ecol Sociobiol 70:797–808

Koch F, Signer J, Kappeler PM, Fichtel C (2016b) The role of the residence-effect on the outcome of intergroup encounters in Verreaux's sifakas. Sci Rep 6:28457

Lindell C (1996) Patterns of nest usurpation: whey should species converge on nest niches? Condor 98:464–473

Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. Science 341:526–530

Maher CR, Lott DF (1995) Definitions of territoriality used in the study of variation in vertebrate spacing systems. Anim Behav 49:1581–1597

Markham AC, Alberts SC, Altmann J (2013) Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population. Anim Behav 84:399–403

Markham AC, Alberts SC, Altmann J (2016) Haven for the night: sleeping site selection in a wild primate. Behav Ecol 27:29–35

Matsuda I, Tuuga A, Bernard H (2011) Riverine refuging by proboscis monkeys (*Nasalis larvatus*) and sympatric primates: implications for adaptive benefits of the riverine habitat. Mamm Biol 76:165–171

McCauley DJ, Graham SI, Dawson TE, Power ME, Ogada M, Nyingi WD, Githaiga JM, Nyunja J, Hughey LF, Brashares JS (2018) Diverse effects of the common hippopotamus on plant communities and soil chemistry. Oecologia 188:821–835

McNab BK (1963) Bioenergetics and the determination of home range size. Am Nat 97:133–140

Milton K, May ML (1976) Body weight, diet and home range area in primates. Nature 259:459–462

Mitani JC, Rodman PS (1979) Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. Behav Ecol Sociobiol 5:241–251

Nievergelt CM, Mutschler T, Feistner ATC (1998) Group encounters and territoriality in wild Alaotran gentle lemurs (*Hapalemur griseus alaotrensis*). Am J Primatol 46:251–258

Oates JF (1977) The social life of a black-and-white colobus monkey, *Colobus guereza*. Z Tierpsychol 45:1–60

Olupot W, Waser PM (2001) Activity patterns, habitat use and mortality risks of mangabey males living outside social groups. Anim Behav 61:1227–1235

Palminteri S, Peres CA (2012) Habitat selection and use of space by bald-faced sakis (*Pithecia irrorata*) in southwestern Amazonia: lessons from a multiyear multigroup study. Int J Primatol 33:401–417

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

Pasternak G, Brown LR, Keinzle S, Fuller A, Barrett L, Henzi SP (2013) Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. Koedoe 55:1078

Payne HFP, Lawes MJ, Henzi SP (2003) Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). Behaviour 140:453–471

Pearce F, Carbone C, Cowlishaw G, Isaac NJB (2013) Space-use scaling and home range overlap in primates. Proc R Soc B 280:20122122

Pebesma EJ, Bivand RS (2005) Classes and methods for spatial data in R. R News 5:9–13

Peres CA (1992) Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. Behaviour 123:220–246

Person DK, Hirth DH (1991) Home range and habitat use of coyotes in a farm region of Vermont. J Wildl Manag 55:433–441

Pitelka FA (1959) Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. Condor 61:233–264

Potts KB, Baken E, Levang A, Watts DP (2016) Ecological factors influencing habitat use by chimpanzees at Ngogo, Kibale National Park, Uganda. Am J Primatol 78:432–440

Potts JR, Lewis MA (2014) How do animal territories form and change? Lessons from 20 years of mechanistic modelling. Proc R Soc B 281: 20140231

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project, https://qgis.osgeo.org. Accessed 15 May 2020

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 15 May 2020

Radford AN, du Plessis M (2004) Green woodhoopoe *Phoeniculus purpureus* territories remain stable despite group-size fluctuations. J Avian Biol 35:262–268

Rasoloharijaona S, Rakotosamimanana B, Randrianambinina B, Zimmerman E (2003) Pair-specific usage of sleeping sites and their implications for social organization in a nocturnal Malagasy primate, the Milne-Edwards' sportive lemur (*Lepilemur edwardsi*). Am J Phys Anthropol 122:251–258

Reichard U (1998) Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). Am J Primatol 46:35–62

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

Schoener TW (1968) Sizes of feeding territories among birds. Ecology 49:123–141

Sekulic R (1982) Daily and seasonal patterns of roaring and spacing in four red howler *Alouatta seniculus* troops. Folia Primatol 39:22–48

Stamps JA, Krishnan VV (2001) How territorial animals compete for divisible space: a learning-based model with unequal competitors. Am Nat 157:154–169

Strong MJ, Sherman BL, Riehl C (2018) Home field advantage, not group size, predicts outcomes of intergroup conflicts in a social bird. Anim Behav 143:205–213

Struhsaker TT (1967a) Social structure among vervet monkeys (*Cercopithecus aethiops*). Behaviour 29:83–121

Struhsaker TT (1967b) Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Reserve, Kenya. Ecology 48: 891–904

Suire A, Isbell LA, Bidner LR, Shinoda Y, Akasaka M, Matsumoto-Oda A (in press) Influence of rainfall on sleeping site choice by a group of anubis baboons (Papio anubis). Am J Primatol

Sunquist ME, Sunquist FC (1989) Ecological constraints on predation by large felids. In: Gittleman JL (ed) Carnivore behavior, ecology, and evolution. Cornell University Press, New York, pp 281–324

Tallents LA, Randall DA, Williams SD, Macdonald DW (2012) Territory quality determines social group composition in Ethiopian wolves *Canis simensis*. J Anim Ecol 81:24–35

Thaker M, Vanak AT, Owen CR, Ogden MB, Neimann SM, Slotow R (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology 92:398–407

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T, Bartlam-Brooks H, Bayarbaatar B, Belant JL, Bertassoni A, Beyer D, Bidner L, van Beest FM, Blake S, Blaum N, Bracis C, Brown D, de Bruyn PJN, Cagnacci F, Calabrese JM, Camilo-Alves C, Chamaillé-Jammes S, Chiaradia A, Davidson SC, Dennis T, DeStefano S, Diefenbach D, Douglas-Hamilton I, Fennessy J, Fichtel C, Fiedler W, Fischer C, Fischhoff I, Fleming CH, Ford AT, Fritz SA, Gehr B, Goheen JR, Gurarie E, Hebblewhite M, Heurich M, Hewison AJM, Hof C, Hurme E, Isbell LA, Janssen R, Jeltsch F, Kaczensky P, Kane A, Kappeler PM, Kauffman M, Kays R, Kimuyu D, Koch F, Kranstauber B, LaPoint S, Leimgruber P, Linnell JDC, López-López P, Markham AC, Mattisson J, Medici EP, Mellone U, Merrill E, de Miranda Mourão G, Morato RG, Morellet N, Morrison TA, Díaz-Muñoz SL, Mysterud A, Nandintsetseg D, Nathan R, Niamir A, Odden J, O'Hara RB, Oliveira-Santos LGR, Olson KA, Patterson BD, Cunha de Paula R, Pedrotti L, Reineking B, Rimmler M, Rogers TL, Rolandsen CM, Rosenberry CS, Rubenstein DI, Safi K, Saïd S, Sapir N, Sawyer H, Schmidt NM, Selva N, Sergiel A, Shiilegdamba E, Silva JP, Singh N, Solberg EJ, Spiegel O, Strand O, Sundaresan S, Ullmann W, Voigt U, Wall J, Wattles D, Wikelski M, Wilmers CC, Wilson JW, Wittemyer G, Zięba F, Zwijacz-Kozica T, Mueller T (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359:466–469

Van Belle S, Estrada A (2020) The influence of loud calls on intergroup spacing mechanism in black howler monkeys (*Alouatta pigra*). Int J Primatol 41:26–286

Van Cleave E, Bidner LR, Ford AT, Caillaud DC, Wilmers CC, Isbell LA (2018) Diel patterns of movement activity and habitat use by leopards (*Panthera pardus pardus*) living in a human-dominated landscape in Central Kenya. Biol Conserv 226:224–237

VanderWaal KL, Wang H, McCowan B, Fushing H, Isbell LA (2014) Multi-level social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). Behav Ecol 25:17–26

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in Southeast Asian langurs: resource defense or mate defense? Am J Primatol 26:233–242

Wahungu GM (2001) Common use of sleeping sites by two primate species in Tana River, Kenya. Afr J Ecol 39:18–23

Wartmann FM, Juarez C, Fernandez-Duque E (2014) Size, site fidelity, and overlap of home ranges and core areas in the socially monogamous owl monkey (*Aotus azarae*) of northern Argentina. Int J Primatol 35:919–939

Waser PM, Jones WT (1983) Natal philopatry among solitary mammals. Q Rev Biol 58:355–390

Wikelski M, Kays R (2017) Movebank: archive, analysis and sharing of animal movement data, https://www.movebank.org. Accessed 2 Feb 2018

Willems EP, Arseneau TJM, Schleuning X, van Schaik CP (2015) Communal range defence in primates as a public goods dilemma. Philos Trans R Soc B 370:20150003

Willems EP, Hellriegel B, van Schaik CP (2013) The collective action problem in primate territory economics. Proc R Soc B 280: 20130081

Wolff JO (1993) Why are female small mammals territorial? Oikos 68: 364–370

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Wrangham RW, Crofoot M, Lundy R, Gilby I (2007) Use of overlap zones among group-living primates: a test of the risk hypothesis. Behaviour 144:1599–1619

Young TP, Okello B, Kinyua D, Palmer TM (1997) KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. Afr J Range For Sci 14:92–104