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Neighboring groups and habitat edges modulate range use in Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*)

Luke Gibson · Andreas Koenig

Abstract An animal's use of space may be strongly influenced by habitat edges and neighboring conspecifics encountered in and around its home range. Habitat edges are known to affect species density and distribution, but their impact on home range use is largely unknown. Additionally, among large animals, interactions with neighbors become particularly important as increasing home range size leads to decreasing exclusivity of resource use, but the effect of neighbors on home range use remains poorly understood. Here, we examine the influence of neighbors and habitat edges on the ranging patterns of three groups of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) in northeast Thailand over a period of more than 2 years. The study animals occupied dry evergreen forest, and adjacent patches of dry dipterocarp forest created a habitat edge and formed barriers between some groups. We found that the use of home range interiors was 50–90% higher than the border areas, indicating concentrated use of resources within the home range. The use of peripheral areas was influenced by social organization, the presence of neighboring groups, and forest edges. While one multimale group showed no particular habitat preference, two single-male groups preferred areas bordering dry dipterocarp habitat and avoided areas

bordering neighboring groups, suggesting that the threat of neighbors mediated border presence. Additionally, groups may have been attracted to the forest edge, where conspecific competitors are absent and increased sunlight may increase resource abundance and/or quality. This study revealed that the use of border areas can be modulated by neighboring groups and habitat edges, thereby adding to our understanding of home range use among territorial species in heterogeneous habitats.

Keywords Edge effects · Home range use · Neighbor avoidance · Territory borders

Introduction

An animal's home range size is determined by its metabolic needs and therefore scales allometrically with body size (McNab 1963; Damuth 1981a; Nunn and Barton 2000), and is further influenced by trophic position as well as social and territorial behavior (Damuth 1981b; Kelt and Van Vuren 2001; Mitchell and Powell 2004; Hamilton et al. 2007). However, at increasing scales, home range boundaries become more difficult to defend from intrusion by neighbors, and the resulting loss of resources to neighbors may explain the disproportionately large home range sizes observed in large animals (Jetz et al. 2004). As large-bodied animals may be unable to effectively defend their home ranges, it is uncertain how they may allocate their time in order to most effectively utilize the limited resources contained within their home range.

Interactions with neighbors may influence both the size of an animal's home range as well as an animal's use of its home range, but unfortunately, these factors remain poorly understood (e.g., Wrangham et al. 2007). In species with established territories, groups or individuals may avoid

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conflicts with known neighbors (Fisher 1954; Ydenberg et al. 1988; Temeles 1994), leading to mutual avoidance of neighbors' ranges (Shillito 1963; Waser 1976; Gorman and Stone 1990). Underuse of home range boundaries or overlap zones of known neighbors, as reported in several studies of carnivores and primates (e.g., Terborgh 1983; Chapman 1990; Herbinger et al. 2001; Samson and Huot 2001; Mech and Harper 2002; Kelly 2005), may also be a strategy to avoid hostile and potentially lethal intergroup interactions (Wilson 1975; Kelly 2005; Wrangham et al. 2007; Mitani et al. 2010). However, the avoidance of neighboring groups may depend on population density (Barrett and Lowen 1998), level of previous punishment (Sih and Mateo 2001; Stamps and Krishnan 2001), and strength of neighbors (e.g., group size, Müller and Manser 2007). In non-human primates, low encounter frequencies are usually attributed to interindividual or intergroup avoidance (Curtin and Chivers 1978; Curtin 1980), specifically when encounter frequencies are less common than expected based on random walk models (Waser 1976; Barrett and Lowen 1998; Hutchinson and Waser 2007). In these ways, interactions with neighboring groups may strongly influence an animal's use of home range boundaries adjacent to neighboring groups.

In addition to interactions with neighboring groups, habitat edges (i.e., discontinuous habitat features; see, e.g., Lidicker 1999) may also help to determine an animal's home range use. Habitat edges often form the boundary of an animal's home range (overview in Desrochers and Fortin 2000) and, for some edge-reliant species, may actually determine the size of its home range. For example, pumas use edge habitat to hunt and require a certain minimum amount of edge habitat to establish home ranges (Laundre and Loxterman 2007). Other species respond to habitat edges by increasing in abundance (Goosem 2000), frequently due to increased resource abundance or quality (Malcolm 1997; Malcolm and Ray 2000; Laurance et al. 2002; Lambert et al. 2006). Similarly, in fragmented landscapes, forest edges can support higher abundances of folivorous primates (Onderdonk and Chapman 2000; Lehman et al. 2006), likely due to increased exposure to sunlight and the associated increased quantity and quality of leaves (Ganzhorn 1995). Alternatively, many species decrease in abundance in habitat edges (e.g., Laurance et al. 2002). While many studies describe the impact of habitat edges on the density and distribution of species, the effects of edges on behavioral ecology are less clear (Lima and Zollner 1996), even though habitat edges appear to be an important factor in determining an animal's home range use.

Given the potential importance of both neighbors and habitat edges on home range use, we incorporated both factors into an analysis of the ranging habits of three groups of wild Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) in northeast Thailand over a period of more

than 2 years. Phayre's leaf monkeys are mid-sized monkeys (Smith and Jungers 1997) belonging to the subfamily of Colobinae characterized by ruminant-like digestion (Bauchop and Martucci 1968). Consequently, leaves dominate their diet (46%), but a substantial part is also (predominantly unripe) fruits and seeds (Borries et al. 2011; Koenig and Borries 2012). In the study population, groups range in size between 6 and 33 animals; 48% of groups contain one adult male (one-male groups), and 52% contain 2–5 adult males (multimale groups; Koenig and Borries 2012). Female dispersal is common (Borries et al. 2004; Koenig et al. 2004) and often occurs during aggressive intergroup encounters that occur at a minimum rate of one encounter per 5 days. During such encounters, males behave aggressively, and females may switch groups, preferentially into multimale groups (Koenig, Borries, Larney, Lu, and Ossi, unpublished).

Here, we investigate how territorial borders, habitat edges, and the number of males per group influenced home range use, asking whether the leaf monkeys used different home range areas in proportion to the size of those areas and which factors best predicted the use of home range border areas. We predicted that the leaf monkeys (1) used home range interiors more intensively than peripheries, but that (2) within peripheral areas, they preferentially used forest edges bordering dry dipterocarp habitat and (3) avoided areas that bordered the ranges of neighboring groups. We made our second prediction because dry dipterocarp habitat is much more open than evergreen forest and increased sunlight may yield increased resource quantity or quality at the transition from evergreen forest to dry dipterocarp habitat. We further suggested that our third prediction should be more evident in one-male groups than in multimale groups as multimale groups may be less influenced by the presence of neighboring groups because they have numerical superiority over single-male groups and likely have at least parity with other multimale groups.

Methods

Study site and population

The study was conducted in Phu Khieo Wildlife Sanctuary (16°5′–16°35′N, 101°20′–101°55′E), northeast Thailand. The sanctuary covers 1,560 km² and is part of the Western Isaan Forest Complex (ca. 6,000 km²). The study site at Huai Mai Sot Yai (16°27′N, 101°38′E) is elevated 600–800 m above sea level. The study site itself as well as the areas to the north, east, and west consist of primary dry evergreen forest, while some areas to the south of the study site consist of patches of dry dipterocarp forest. In contrast to the dry evergreen forest with a tree and climber density of

523 stems per hectare (Koenig and Borries, unpublished), the dry dipterocarp habitat is open with a grassy layer and a discontinuous canopy. The only paved road within the sanctuary passes through patches of dry dipterocarp forest along the southern edge of the study site (see map in Fig. 1). Additional descriptions of the study site are given in Borries et al. (2002) and Koenig and Borries (2012).

Our study subjects were three habituated groups of wild Phayre's leaf monkeys, which primarily inhabit the dry evergreen forest of Huai Mai Sot Yai. However, they also used the edge between dry evergreen and dry dipterocarp forest, and they may (very rarely) cross small patches of dry dipterocarp forest on the ground. During the course of the study, group membership varied; PS consisted on average of 12.1

Fig. 1 Map of the 95% kernel home ranges and 100-m buffers of the three study groups, showing **a** the GPS locations of the groups and **b** the different peripheral areas bordering dry dipterocarp habitat (dip), neighboring leaf monkey groups (neighbors), and both (dip neighbors). The map is based on Universal Transverse Mercator (UTM, Zone 47Q) readings with the GPS set to the Indian–Thailand map datum
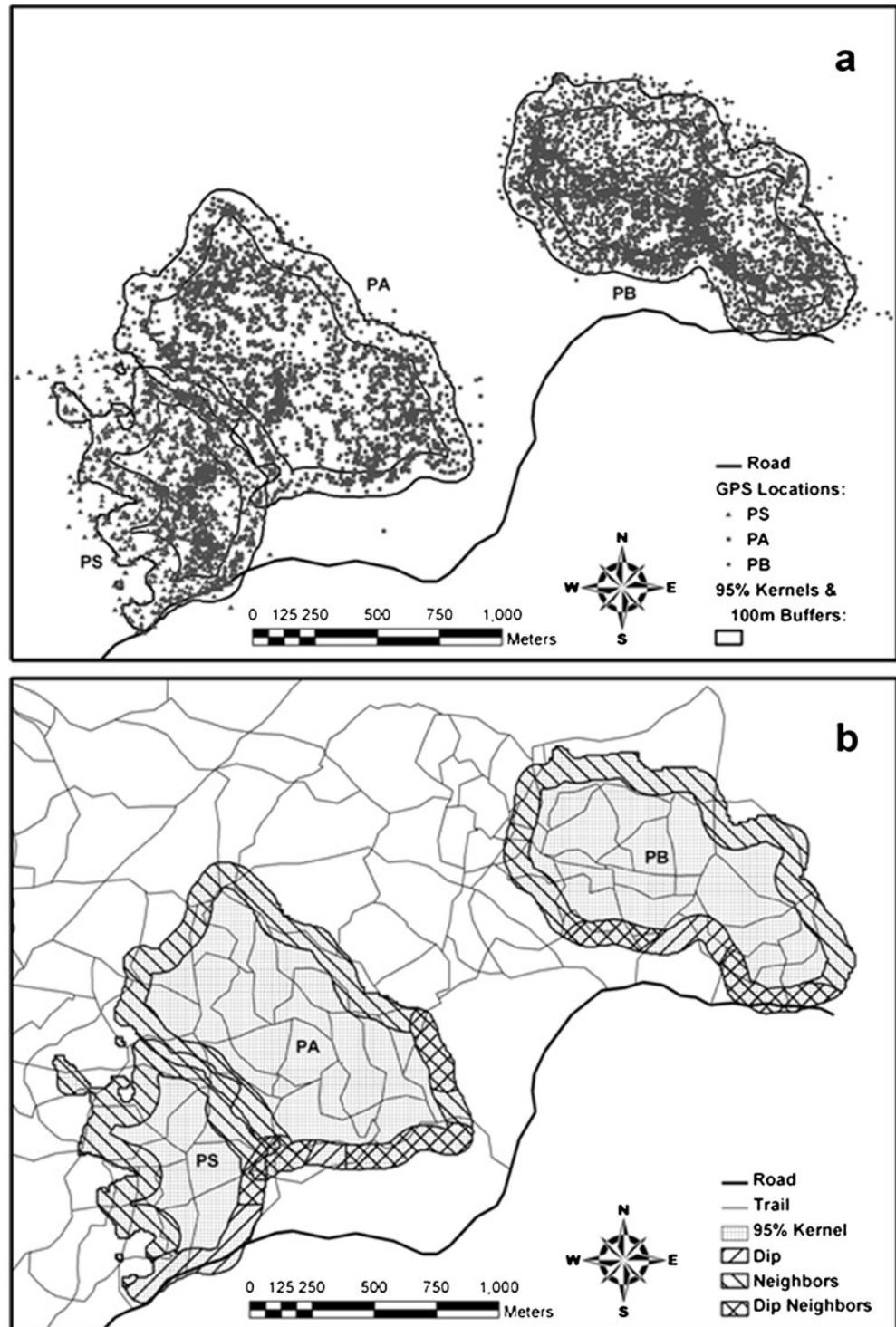
individuals, PA of 17.3 individuals, and PB of 24.9 members (for adult composition, see Table 1). Data presented here cover more than 2 years from March 2004 to June 2006.

Data collection and analysis

To characterize weather conditions (see below), temperature data were collected every 2 h via data loggers (HOBO® H8 Pro) located in the forest within the home range of group PA. Rainfall was measured via a flow-through automatic rain gauge (HOBO® data logging rain gauge) located at a ranger station ca. 5 km from the study site to be protected from elephants. Temperature data were available for a period of 5 years from January 2001 to December 2005, and rainfall data were available for 3 years from January 2003 to December 2005 (for a general climate diagram, see Grassman et al. 2005).

Each group was followed from dawn (when the monkeys became active) to dusk (when they stopped moving and settled for rest) for at least five complete consecutive days every month. In total, we followed group PS for 162 days, PA for 311 days, and PB for 440 days. At dawn and dusk and every half hour in between, a GPS point was taken at the approximate center of the group using a handheld Garmin® GPS 12 or 12 XL. All points with errors greater than 10.0 m were discarded.

We mapped all GPS points in ArcView 3.2 and used the Animal Movement extension (Hooge and Eichenlaub 2000) to create 95% fixed kernels to represent the home ranges for each group (Fig. 1; Worton 1989). To define the border and non-border areas of the home ranges, we created a 100-m buffer inside the edge of the kernels; we classified this as the border area and the remaining interior area as the non-border area. We further characterized the border areas based on whether they bordered (1) dry dipterocarp habitat (dip) and (2) known or suspected neighboring leaf monkey groups (neighbor), both of which had been previously mapped using GPS. Thus, the home ranges were divided into distinct polygons representing non-border areas and different border areas bordering dry dipterocarp habitat and/or neighboring leaf monkey groups (see map in Fig. 1b). The 100-m buffer was selected based on the presumed detection distance of

Table 1 Group composition and home range size of three Phayre's leaf monkey groups

Group	N members	N adult males	N adult females	Home range size [ha]
PS	12.1 (9–16)	1	4.2 (4–5)	52.2
PA	17.3 (14–20)	2.2 (2–3)	4.4 (3–6)	102.5
PB	24.9 (23–28)	1	10.8 (10–12)	92.4

Reported are the average values (and range) for group composition and the 95% kernel home range sizes for each group over the entire study period (March 2004 to June 2006)

conspecifics (neighbors or solitary individuals). However, we repeated the entire procedure while setting the buffer distance at 50 m, but this did not affect the results (not shown here).

An additional factor which may have influenced the use of specific border areas was a paved road, which passed by the southern part of the ranges of all three groups (Fig. 1). The monkeys crossed the road very rarely, either arboreally or on the ground, and thus, the road could represent a barrier that influenced the leaf monkeys' use of different border areas. However, since the road was built almost entirely along the dry ridges of the open dipterocarp habitat, we were unable to differentiate between the effect of the road and that of the dry dipterocarp habitat on the monkeys' home range use (the two variables are statistically singular, and as such redundant; Tabachnick and Fidell 2001). Separate tests (see the description of ANCOVAs below) using one or the other of these factors as independent variables led to similar results. However, the road, which measured only 5 m wide and harbored very little traffic, might be of minor importance compared to the dry dipterocarp forest, which, in some patches, extends for hundreds of meters and therefore presents a more significant barrier to movements of leaf monkeys. At the same time, the slight opening of the canopy at the road would reinforce the effect of increased sunlight at the edge between dry evergreen and dry dipterocarp forest.

To examine the leaf monkeys' use of their home ranges, we used two separate procedures. To investigate avoidance or preference of areas in relation to their size, we calculated the total number of GPS points located within each of the different areas. For this analysis, all GPS points falling outside the 95% kernels were discarded. In each polygon, we calculated the density of GPS points per hectare. We then used the chi-squared test (Sokal and Rohlf 1995) to test whether the frequency of GPS points in each distinct home range area was proportional to its size. Because GPS points were collected consecutively during follows, consecutive points may not be independent. To address this issue, we repeated the analysis by randomly resampling the dataset, selecting one GPS point per day, and calculated the mean frequencies and 95% confidence intervals based on 10,000 bootstrap samples. As the leaf monkeys travel on average 1,018 m per day (Carl 2009) and home ranges are between ca. 50 and 100 ha (see below), resampling one point per day assures that samples are independent.

To further compare the frequency of border area use across groups and seasons and to identify the factors influencing the frequency of use, we ran general linear model ANCOVAs using polygon size as a covariate (Quinn and Keough 2002). We first summarized the number of GPS points per group, polygon, and season ($N=35$ data points per group). Season was divided into three categories: cold dry: November–February; hot wet: March–April; and hot

very wet: May–October. This subdivision is based on monthly and yearly averages and corresponding 95% confidence limits, and conforms to the phenology, given that leaf flushing starts in March and fruit availability peaks between May and September. We calculated the percent of time spent in each border area (with total border use set as 100%) and arcsine transformed the values (Sokal and Rohlf 1995). In addition to the covariate polygon size, we intended to use social organization (one male vs. multimale), season, dip, and neighbors as categorical independent factors in the ANCOVA. However, not all combinations occurred for both one-male and multimale groups, which did not allow us to calculate a full model and to incorporate group ID as random factor. Hence, we ran two separate models: first, to test for the effects of polygon characteristics and season (factors: season, dip, neighbors) and, second, to test for the effects of social organization and season (factors: season, social organization, neighbors). Because the data were collected from the same groups over time, seasonal data might not be independent. Hence, we also ran general linear mixed model ANCOVAs with season as random factor, but the results changed only marginally (see below).

All statistical analysis was performed either in the statistical program R version 2.11.1 (R Development Core Team 2010), with STATISTICA 6.1 (© StatSoft Inc. 1984–2003), or with STATISTICA 10 (© StatSoft Inc. 1984–2011).

Results

GPS database and home range size

In total, 18,618 GPS data points were collected. Of these, 2,282 points had errors exceeding our 10.0-m criterion or contained insufficient information and were discarded. The remaining 16,336 points consisted of 3,235 points from PS, 4,537 points from PA, and 8,564 points from PB. The higher number for PB is due to the fact that this group was followed almost daily in 2006 because of an additional research project. These GPS points were used to create 95% kernel home ranges for each group (Fig. 1). The home range sizes varied; PS, the smallest group, had a home range size of 52.2 ha, while the medium-sized group PA had a home range of 102.5 ha, and the largest group PB had a home range of 92.4 ha (Table 1). The home ranges of neighboring groups PS and PA overlapped by 3.00 ha, representing 5.75% and 2.93% of their total home ranges, respectively. For the following analysis of range use, the points located outside the kernels were discarded, leaving 3,011 points for PS, 4,464 points for PA, and 8,359 points for PB.
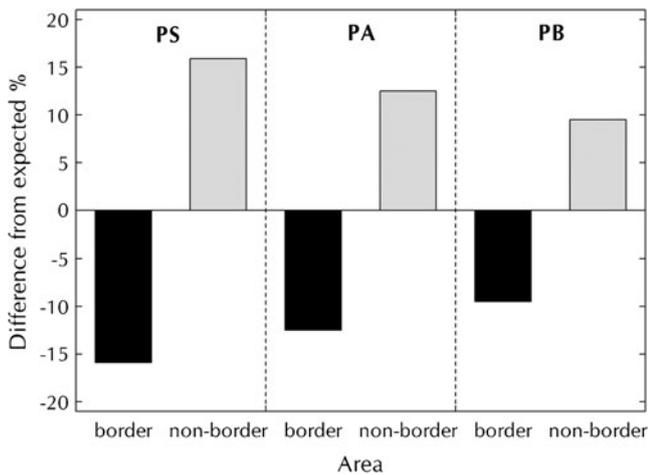
Use of non-border and border areas

For each group, we compared the number of GPS points in the non-border interior and in the 100-m border area (Table 2). In all cases, the null hypothesis that the monkeys used areas in direct proportion to their size was rejected (X^2 values: PS: 327.43; PA: 293.45; PB: 308.89; all cases: $P<0.001$); the density of points in the interior areas was between 50% and 90% higher than the density of points in border areas. The observed percentages for points in the border versus the non-border areas differed by 9.5% to 16% from the expected values based on the size of the areas (Fig. 2). The frequency of points in non-border and border areas changed little after resampling one GPS point per day (Table 2), suggesting that the results presented previously are not biased due to spatial autocorrelation. Again, in all instances, the resampled frequencies were significantly different from expected resampled

Table 2 The use of non-border and 100-m border areas of three Phayre's leaf monkey groups

Group	Area category	Size of area [ha]	Observed frequency	Observed density	Expected frequency	Resampled frequency	Expected resampled frequency
PS	Border	32.97 (63.17%)	1,423 (47.26%)	43.16	1,902	70.33 (61–79) (49.53%)	89.70
	Non-border	19.23 (36.83%)	1,588 (52.74%)	82.58	1,109	71.67 (63–81) (50.30%)	52.30
PA	Border	40.75 (39.74%)	1,214 (27.20%)	29.79	1,774	56.10 (46–66) (27.37%)	81.47
	Non-border	61.78 (60.26%)	3,250 (72.80%)	52.61	2,690	148.90 (139–159) (72.63%)	123.53
PB	Border	39.38 (42.61%)	2,767 (33.10%)	70.26	3,562	126.27 (112–140) (34.21%)	157.22
	Non-border	53.05 (57.39%)	5,592 (66.90%)	105.41	4,797	242.73 (229–257) (65.78%)	211.78

Reported are sizes of border and non-border areas (and percentage of total area), observed frequencies of use (and percentage of total use, based on the number of GPS points recorded per area) and densities (number of GPS points per hectare), and expected frequencies of use (based on the area's percentage of total area). We recalculated the frequencies by randomly sampling one GPS point from each day (PS: 142 days; PA: 205 days; PB: 369 days); resampled frequencies report the mean (and 95% CI) of 10,000 bootstrap samples. In all cases, observed frequencies were significantly different from expected frequencies. Resampled frequencies were similar to observed frequencies, and in all cases, the resampled frequencies were significantly different from expected resampled frequencies
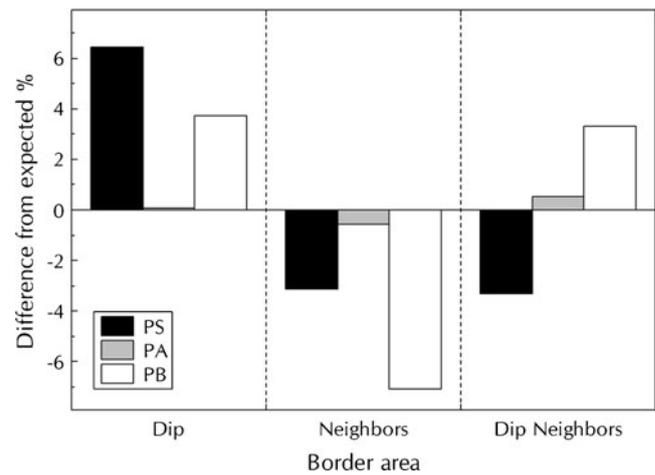
Fig. 2 Difference between observed and expected frequency of use of border and non-border areas for three Phayre's leaf monkey groups. Depicted is the percentage of observed minus expected GPS points recorded in each area for each group

Fig. 3 Difference between observed and expected frequency of use of different border areas for three Phayre's leaf monkey groups. Depicted is the percentage of observed minus expected GPS points recorded in each area for each group. Note that a value for dip-PA exists but it is very close to zero (0.06%)

frequencies based on the area (X^2 values: PS: 11.36; PA: 13.11; PB: 10.62; all cases: $P < 0.001$, except for PB: $P = 0.0011$).

Use of different border areas

To investigate avoidance or preference of areas according to size, we excluded the interior area and compared the frequency of use of the different border areas (Table 3). Only for group PA did we find no significant difference between expected and observed frequencies ($X^2 = 0.19$, $P = 0.91$). However, for PS and PB, the density of points in the

different border areas varied greatly and differed significantly from the expected values based on area (PS: $X^2 = 67.60$, $P < 0.001$; PB: $X^2 = 75.26$, $P < 0.001$). In PS and PB, the density of points was highest in the area bordering the habitat edge. It must be noted that the dry dipterocarp forest which formed the habitat edge in the study site was also the site of a small road, which could have produced the observed ranging patterns. However, because the road overlapped with the dry dipterocarp habitat, we cannot distinguish between the effects of the two. For PB, the density of points was lowest in the area bordering neighboring groups, and for PS, the density was significantly lower

Table 3 The use of 100-m border areas of three Phayre's leaf monkey groups

Group	Area category	Size of area [ha]	Observed frequency	Observed density	Expected frequency	Resampled frequency	Expected resampled frequency
PS	Dip	3.44 (10.42%)	240 (16.87%)	69.77	148	18.84 (15–23) (15.92%)	12.33
	Neighbors	23.76 (72.08%)	981 (68.94%)	41.29	1,026	84.15 (80–88) (71.12%)	85.29
	Dip neighbors	5.77 (17.50%)	202 (14.20%)	35.01	249	15.33 (10–20) (12.96%)	20.71
PA	Dip	1.45 (3.56%)	44 (3.62%)	30.34	43	8.97 (5–13) (6.23%)	5.13
	Neighbors	27.72 (68.04%)	819 (67.46%)	29.55	826	99.27 (94–105) (68.97%)	97.93
	Dip neighbors	11.57 (28.40%)	351 (28.91%)	30.34	345	35.70 (31–41) (24.80%)	40.87
PB	Dip	3.68 (9.35%)	362 (13.08%)	98.37	259	55.64 (47–65) (18.78%)	27.69
	Neighbors	27.08 (68.75%)	1,707 (61.69%)	63.04	1,902	169.71 (162–178) (57.29%)	203.65
	Dip neighbors	8.63 (21.90%)	698 (25.23%)	80.88	606	70.87 (63–79) (23.93%)	64.89

Reported are sizes of different border areas (and percentage of total border area), observed frequencies of use (and percentage of total use in border area, based on the number of GPS points recorded per area) and densities (number of GPS points per hectare), and expected frequencies of use (based on the area's percentage of total border area). We recalculated the frequencies by randomly sampling one GPS point from each day (PS: 119 days; PA: 148 days; PB: 306 days); resampled frequencies report the mean (and 95% CI) of 10,000 bootstrap samples. For groups PS and PB, observed frequencies were significantly different from expected frequencies. Resampled frequencies were similar to observed frequencies, and for PB, resampled frequencies were significantly different from expected resampled frequencies

in all areas bordering neighboring leaf monkey groups (neighbors and dip neighbors, Fig. 3). Resampled frequencies were similar to the observed frequencies (Table 3), again suggesting that the aforementioned results are not biased due to spatial autocorrelation. For PB, the resampled frequencies were significantly different from expected resampled frequencies based on the area, suggesting that resampled frequencies were proportional to area (PS: $X^2 =$ 4.85, $P=0.088$; PA: $X^2=3.55$, $P=0.17$; PB: $X^2=34.41$, $P<0.001$).

Our ANCOVA analysis showed a strong, positive relationship between size of border area and frequency of use for all three groups (Fig. 4). In both ANCOVAs, the size of the polygon was the main predictor of use of the border areas (Table 4); however, other factors played an important role, too. When testing polygon characteristics and season, the presence/absence of dry dipterocarp habitat ($P<0.05$) and the presence/absence of neighbors ($P<0.02$) each or in combination affected border area use (Table 4; Fig. 5). Most prominently, areas bordering neighbors but not dry dipterocarp forest were least frequently used, while all other areas were used more frequently (interaction effect of dip and neighbors, $P<0.001$). Additionally, areas bordering dry dipterocarp forest were used more frequently in the hot-wet season (March–April), coinciding with the start of the leaf flush in any given year (interaction effect of dip and season, $P<0.001$). Rerunning the analysis as a mixed model with season as random factor led to similar results, except that the effect of the dipterocarp forest (as main factor) became non-significant ($P=0.12$), while the interaction effects with this variable and neighbors as well as season remained significant.
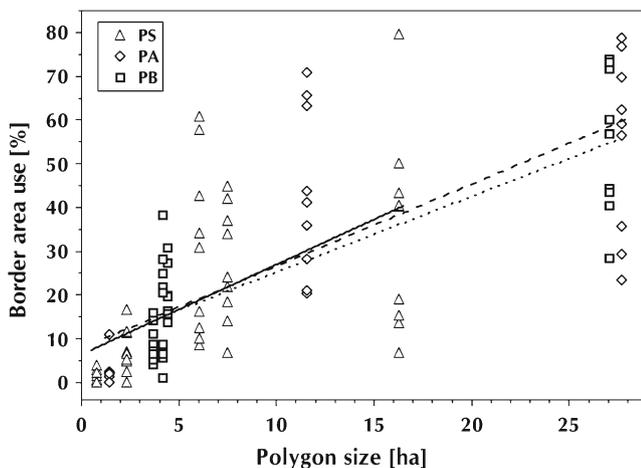
Fig. 4 Percentage of border area use in relation to polygon size for each of the three groups. Plotted are values per season, polygon, and group ($N=36$ per group; see text for definition of seasons). *Regression lines* added for demonstration purposes only (PS, *solid line*: $y=6.45+2.06 \times x$; PA, *hatched line*: $y=7.89+1.87$; PB, *dotted line*: $y=7.96+1.73$)

Table 4 Results of general linear model ANCOVAs for the effects of border area characteristics (polygon size, dip (presence–absence), neighbors (presence–absence)), season (cold-dry, hot-wet, hot-very wet), and social organization (one-male–multimale) on percent use of border polygons (arcsine transformed). Significant *P*-values are given in bold

	df	MS	F	P
Dipterocarp, neighbors, and season				
Polygon size [ha]	1	1.838	61.91	**< 0.001**
Season	2	0.022	0.724	0.487
Dip	1	0.117	3.94	**0.0499**
Neighbors	1	0.172	5.80	**0.0180**
Season × dip	2	0.254	8.54	**< 0.001**
Season × neighbors	2	0.010	0.35	0.707
Dip × neighbors	1	0.631	21.25	**< 0.001**
Season × dip × neighbors	2	0.001	0.04	0.958
Error	95	0.030		
Social organization, neighbors, and season				
Polygon size [ha]	1	2.126	54.60	**< 0.001**
Social organization	1	0.053	1.36	0.246
Season	2	0.003	0.07	0.936
Neighbors	1	0.304	7.80	**0.006**
Social organization × season	2	0.0003	0.01	0.992
Social organization × neighbors	1	0.353	9.06	**0.003**
Season × neighbors	2	0.005	0.14	0.869
Social organization × season × neighbors	2	0.004	0.11	0.900
Error	95	0.039		

These relationships changed in the second ANCOVA that used the independent variable social organization instead of dry dipterocarp habitat (Table 4). Overall, areas bordering neighboring groups were used more frequently than areas not bordering neighbors ($P<0.01$; Fig. 6); however, this effect varied among groups: The one-male groups spent much more time in areas without neighbors than the multimale group, but this relationship was reversed in border areas with neighbors (interaction effect of social organization and neighbors; $P<0.01$). All other factors including season remained non-significant (Table 4). Rerunning the analysis as a mixed model with season as random factor led to similar results, except that the effect of social organization (as main factor) became significant ($P<0.001$), underscoring the importance of this variable.

Discussion

Our results show that Phayre's leaf monkeys spent considerably more time in the interior of their home ranges than in border areas. The concentrated use in the center of a home range is a pattern commonly observed in primates and other
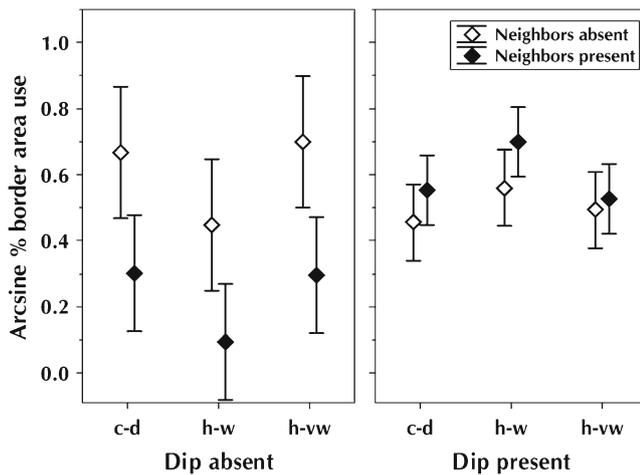
Fig. 5 Percentage of border area use (arcsine transformed) in relation to edge characteristics (the presence or absence of dip; the presence or absence of neighbors) across three seasons (*c-d* cold-dry, *h-w* hot-wet, *h-vw* hot-very wet). Depicted are the least square means and 95% confidence intervals calculated at the covariate means (polygon size = 9.42 ha). The figure shows the interaction of all three variables with $F_{2,\ 95}=0.04$, $P=0.958$ (for further test values, see Table 4)

animals (e.g., Ganey and Balda 1989; Zhang 1995; Di Bitetti 2001; Guerra-Castro et al. 2007), and in this study, it could be due to the presence of important sleeping sites (see also Chapman et al. 1989). This pattern closely follows Terborgh's (1983) suggestion that animals will show concentrated use of resources that occur in sparsely distributed patches. Alternatively, the concentrated use of home range interiors may be explained by the risk avoidance hypothesis, whereby groups minimize conflict with neighbors by avoiding parts of their home ranges that overlap ranges of
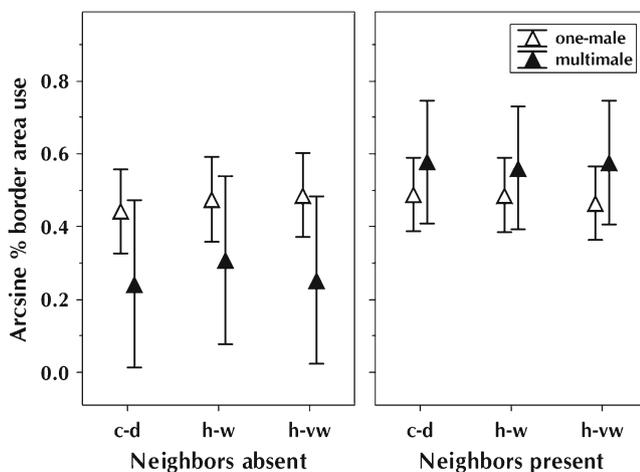
Fig. 6 Percentage of border area use (arcsine transformed) in relation to social organization (one male vs. multimale) and the presence or absence of neighbors across three seasons (*c-d* cold-dry, *h-w* hot-wet, *h-vw* hot-very wet). Depicted are the least square means and 95% confidence intervals calculated at the covariate means (polygon size = 9.42 ha). The figure shows the interaction of all three variables with $F_{2,\ 95}=0.11$, $P=0.900$ (for further test values, see Table 4)

conspecifics (Wrangham et al. 2007). However, another simpler explanation remains: Regardless of starting and ending points, the majority of possible paths within a home range will traverse the interior, and the interior is thus likely to be more frequently used than peripheral areas (Charles Janson, personal communication). Given this suggestion, the size of an area is probably too simplistic to form an appropriate null model for the expected use of interior vs. peripheral areas, but may represent a valid null model to test for differential use of particular border areas separately.

Among the distinct home range peripheries, we found that different features of the border areas influenced the ranging patterns of Phayre's leaf monkeys. For the two single-male groups (PS and PB), the use of areas bordering dry dipterocarp habitat was higher than expected, and the use of areas bordering neighboring conspecifics was lower than expected. ANCOVA results support this finding, indicating that the forest edge and the presence of neighbors significantly affected the border use. Combined, our results suggest that the leaf monkeys were attracted to areas bordering dry dipterocarp habitat, particularly during spring, and deterred from areas bordering neighboring groups. However, in the third and only multimale group (PA), this pattern was not found, a discrepancy that we discuss in the next section.

Attraction or avoidance of neighbors

For the two single-male groups, we found that frequency of use among peripheral areas was substantially lower than expected in areas bordering neighboring groups. Interestingly, however, the one group not fitting the pattern of conspecific avoidance was the only group with more than one adult male. This result is further supported by the ANCOVA showing that one-male groups most frequently used border areas without neighbors, while multimale groups were mostly present in areas with neighbors. The strength or number of neighbors often affects a group's avoidance of neighboring groups (Herbinger 2004; Müller and Manser 2007), and our results support this assertion, suggesting that the threat level posed by neighbors mediates the likelihood of border presence (see also Stamps and Krishnan 2001). In the study population, however, where only males participate in intergroup encounters, threat level seems to be determined not by the total size of the group but by the number of adult males. This is in line with game theoretic expectations and findings for other primates that with increasing differences between contestants, the likelihood for encounters decreases (Wilson et al. 2001; Wilson et al. 2002; Kitchen 2004; Kitchen et al. 2004). However, we cannot draw firm conclusions about the effects of male number because we sampled only three groups, only one of which was multimale.

Attractive and repellent edges

The leaf monkeys were apparently attracted to areas bordering the dry dipterocarp habitat, but deterred from areas bordering neighboring groups. Forest edges bordering the open dipterocarp habitat may contain increased resource quantity and/or quality that would attract these primate folivores. Ganzhorn (1995) found that increased light levels in a moderately logged habitat resulted in higher quality leaves and greater abundance of fruit as compared to undisturbed habitats. Although we did not measure sunlight in this study, it is very likely that the edge of the dry evergreen forest next to the open dipterocarp habitat was exposed to greater sunlight than the interior forest, and thus, trees may have contained higher food quantity or quality due to increased productivity. Phenological surveys in the interior and edge areas combined with tests of nutritional quality could test this suggestion.

At the same time, however, the leaf monkeys may also be attracted to areas bordering dry dipterocarp habitat because of reduced competition from neighboring groups. Phayre's leaf monkeys do not normally occupy dry dipterocarp forest, and so, this habitat seems to form a natural barrier between groups (Stamps et al. 1987). Other studies indicate similar effects for natural barriers (Duelli et al. 1990; Nievergelt et al. 1998; Haynes and Cronin 2006). In any case, the hypothesis that intergroup competition influenced home range use was supported by the finding that single-male groups avoided border areas where they could potentially encounter neighbors, but the multimale group showed no preference among the different border areas.

Conclusions

This study showed that home range use, and particularly the use of border areas, is influenced by neighboring groups and habitat edges. For both single-male groups, the use of areas bordering neighboring groups was considerably lower than the use of areas bordering habitat edges. Because intergroup encounters are notoriously rare in many species and hence systematic studies are difficult to conduct (Crofoot et al. 2008), studies on the use of peripheral range areas may overcome this problem.

Habitat and home range use is affected by a plethora of factors, not just a single one (Terborgh 1983; Ims 1988; Eason et al. 1999; Desrochers and Fortin 2000; Nunn and Dokey 2006). In this study, we found that interactions with neighboring groups and the location of habitat edges strongly influenced the use of different home range boundaries. These factors should be incorporated into analyses of ranging patterns, particularly in large species where resource use in home ranges becomes non-exclusive due to competition

with neighbors (Jetz et al. 2004). Our results reveal the potential importance of natural habitat edges to Phayre's leaf monkeys, which preferentially utilize forest edges to avoid competition from neighboring groups and perhaps to gain access to more and/or higher quality food. Further examination of the use of home range boundaries will help us to understand how animals utilize different parts of their home ranges in order to minimize competition with neighbors and exploit limited resources within their home ranges to maximum efficiency.

References

Barrett L, Lowen CB (1998) Random walks and the gas model: spacing behaviour of grey-cheeked mangabeys. Funct Ecol 12:857–865. doi:10.1046/j.1365-2435.1998.00261.x

Bauchop T, Martucci RW (1968) Ruminant like digestion of the langur monkey. Science 161:698–700. doi:10.1126/science.161.3842.698

Borries C, Larney E, Kreetiyutanont K, Koenig A (2002) The diurnal primate community in a dry evergreen forest in Phu Khieo Wildlife Sanctuary, northeast Thailand. Nat Hist Bull Siam Soc 50:75–88

Borries C, Larney E, Derby AM, Koenig A (2004) Temporary absence and dispersal in Phayre's leaf monkeys (*Trachypithecus phayrei*). Folia Primatol 75:27–30. doi:10.1159/000073428

Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A (2011) Primate life histories and dietary adaptations: a comparison of Asian colobines and macaques. Am J Phys Anthropol 144:286–299. doi:10.1002/ajpa.21403

Carl KM (2009) Home range size, daily path length, and territoriality in Phayre's leaf monkeys (*Trachypithecus phayrei*). MA thesis, Stony Brook University

Chapman CA (1990) Association patterns of spider monkeys: the influence of ecology and sex on social organization. Behav Ecol Sociobiol 26:409–414. doi:10.1007/BF00170898

Chapman CA, Chapman LJ, McLaughlin RL (1989) Multiple central place foraging by spider monkeys—travel consequences of using many sleeping sites. Oecologia 79:506–511. doi:10.1007/BF00378668

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. doi:10.1073/pnas.0707749105

Curtin SH (1980) Dusky and banded leaf monkeys. In: Chivers DJ (ed) Malayan forest primates. Ten years in tropical rain forest. Plenum Press, New York, pp 107–145

Curtin SH, Chivers DJ (1978) Leaf-eating primates of Peninsular Malaysia: the siamang and the dusky leaf-monkey. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, pp 441–464

Damuth J (1981a) Home range overlap and species energy use among herbivorous mammals. Biol J Linn Soc 15:185–194. doi:10.1111/j.1095-8312.1981.tb00758.x

Damuth J (1981b) Population density and body size in mammals. Nature 290:699–700. doi:10.1038/290699a0

Desrochers A, Fortin MJ (2000) Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. Oikos 91:376–384. doi:10.1034/j.1600-0706.2000.910218.x

Di Bitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. J Zool 253:33–45. doi:10.1017/S0952836901000048

Duelli P, Studer M, Marchand I, Jakob S (1990) Population-movements of arthropods between natural and cultivated areas. Biol Conserv 54:193–207. doi:10.1016/0006-3207(90)90051-P

Eason PK, Cobbs GA, Trinca KG (1999) The use of landmarks to define territorial boundaries. Anim Behav 58:85–91. doi:10.1006/anbe.1999.1133

Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB (eds) Evolution as a process. Allen and Unwin, London, pp 71–83

Ganey JL, Balda RP (1989) Home-range characteristics of spotted owls in Northern Arizona. J Wildl Manage 53:1159–1165

Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology 76:2084–2096. doi:10.2307/1941683

Goosem M (2000) Effects of tropical rainforest roads on small mammals: edge changes in community composition. Wildl Res 27:151–163. doi:10.1071/WR98091

Gorman ML, Stone RD (1990) Mutual avoidance by European moles *Talpa europaea*. In: MacDonald DW, Müller-Schwarze D, Natynczuk SE (eds) Chemical signals in vertebrates 5. Oxford University Press, New York, pp 367–377

Grassman LI, Tewes ME, Silvy NJ, Kreetiyutanont K (2005) Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in north-central Thailand. J Zool 266:45–54. doi:10.1017/S095283690500659X

Guerra-Castro E, Carmona-Suárez CA, Conde JE (2007) Activity patterns and zonation of the swimming crabs *Arenaeus cribrarius* and *Callinectes ornatus*. J Crustac Biol 27:49–58. doi:10.1651/S-2651.1

Hamilton MJ, Milne BT, Walker RS, Brown JH (2007) Nonlinear scaling of space use in human hunter-gatherers. P Natl Acad Sci USA 104:4765–4769. doi:10.1073/pnas.0611197104

Haynes KJ, Cronin JT (2006) Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos 113:43–54. doi:10.1111/j.0030-1299.2006.13977.x

Herbinger I (2004) Inter-group aggression in wild West African chimpanzees (*Pan troglodytes verus*): mechanisms and functions. Ph.D. thesis, University of Leipzig, Leipzig

Herbinger I, Boesch C, Rothe H (2001) Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Cote d'Ivoire. Int J Primatol 22:143–167

Hooge PN, Eichenlaub B (2000) Animal movement extension to Arc-View, version 2.0. Alaska Science Center—Biological Science Office, U.S. Geological Survey, Anchorage, AK

Hutchinson JMC, Waser PM (2007) Use, misuse and extensions of "ideal gas" models of animal encounter. Biol Rev 82:335–359. doi:10.1111/j.1469-185X.2007.00014.x

Ims RA (1988) Spatial clumping of sexually receptive females induces space sharing among male voles. Nature 335:541–543. doi:10.1038/335541a0

Jetz W, Carbone C, Fulford J, Brown JH (2004) The scaling of animal space use. Science 306:266–268. doi:10.1126/science.1102138

Kelly RC (2005) The evolution of lethal intergroup violence. P Natl Acad Sci USA 102:15294–15298. doi:10.1073/pnas.0505955102

Kelt DA, Van Vuren DH (2001) The ecology and macroecology of mammalian home range area. Am Nat 157:637–645

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Anim Behav 67:125–139. doi:10.1016/j.anbehav.2003.03.007

Kitchen DM, Cheney DL, Seyfarth RM (2004) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197–218. doi:10.1163/156853904322890816

Koenig A, Borries C (2012) Social organization and male residence patterns in Phayre's leaf monkeys. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin. doi:10.1007/978-3-642-22514-7_10

Koenig A, Larney E, Lu A, Borries C (2004) Agonistic behavior and dominance relationships in female Phayre's leaf monkeys—preliminary results. Am J Primatol 64:351–357. doi:10.1002/ajp.20084

Lambert TD, Malcolm JR, Zimmerman BL (2006) Amazonian small mammal abundances in relation to habitat structure and resource abundance. J Mammal 87:766–776

Laundre JW, Loxterman J (2007) Impact of edge habitat on summer home range size in female pumas. Am Midl Nat 157:221–229. doi:10.1674/0003-0031(2007) 157[221:IOEHOS]2.0.CO;2

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Cons Biol 16:605–618. doi:10.1046/j.1523-1739.2002.01025.x

Lehman SM, Rajaonson A, Day S (2006) Lemur responses to edge effects in the Vohibola III Classified Forest, Madagascar. Am J Primatol 68:293–299. doi:10.1002/ajp.20224

Lidicker WZJ (1999) Responses of mammals to habitat edges: an overview. Landsc Ecol 14:333–343. doi:10.1023/A:1008056817939

Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. Trends Ecol Evol 11:131–135. doi:10.1016/0169-5347(96)81094-9

Malcolm JR (1997) Biomass and diversity of small mammals in Amazonian forest fragments. In: Laurance WF, Bierregaard RO (eds) Tropical forest fragments: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, pp 207–222

Malcolm JR, Ray JC (2000) Influence of timber extraction routes on central African small-mammal communities, forest structure, and tree diversity. Cons Biol 14:1623–1638. doi:10.1111/j.1523-1739.2000.99070.x

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

Mech LD, Harper EK (2002) Differential use of a wolf, *Canis lupus*, pack territory edge and core. Can Field Nat 116:315–316

Mitani JC, Watts DP, Amsler SJ (2010) Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Curr Biol 20: R507–R508. doi:10.1016/j.cub.2010.04.021

Mitchell MS, Powell RA (2004) A mechanistic home range model for optimal use of spatially distributed resources. Ecol Model 177:209–232. doi:10.1016/j.ecolmodel.2004.01.015

Müller CA, Manser MB (2007) "Nasty neighbours" rather than "dear enemies" in a social carnivore. P Roy Soc B 274:959–965. doi:10.1098/rspb.2006.0222

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. doi:10.1002/(SICI)1098-2345(1998) 46:3<251::AID-AJP5>3.0. CO;2-H

Nunn CL, Barton RA (2000) Allometric slopes and independent contrasts: a comparative test of Kleiber's law in primate ranging patterns. Am Nat 156:519–533

Nunn CL, Dokey AT-W (2006) Territoriality and parasitism in primates. Biol Lett 2:351–354. doi:10.1098/rsbl.2006.0485

Onderdonk DA, Chapman CA (2000) Coping with forest fragmentation: the primates of Kibale National Park, Uganda. Int J Primatol 21:587–611. doi:10.1023/A:1005509119693

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

R Development Core Team (2010) The R Project for Statistical Computing, version 2.11.1. Available at http://www.R-project.org

Samson C, Huot J (2001) Spatial and temporal interactions between female American black bears in mixed forests of eastern Canada. Can J Zool 79:633–641. doi:10.1139/cjz-79-4-633

Shillito JF (1963) Observations on the range and movements of a woodland population of the common shrew *Sorex araneus* L. Proc Zool Soc Lond 140:533–546. doi:10.1111/j.1469-7998.1963.tb01872.x

Sih A, Mateo J (2001) Punishment and persistence pay: a new model of territory establishment and space use. Trends Ecol Evol 16:477–479. doi:10.1016/S0169-5347(01)02251-0

Smith RJ, Jungers WL (1997) Body mass in comparative primatology. J Hum Evol 32:523–559. doi:10.1006/jhev.1996.0122

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. WH Freeman, New York

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

Stamps JA, Buechner M, Krishnan VV (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. Am Nat 129:533–552

Tabachnick BG, Fidell LS (2001) Using multivariate statistics, 4th edn. Allyn and Bacon, Boston

Temeles EJ (1994) The role of neighbors in territorial systems—when are they dear enemies? Anim Behav 47:339–350. doi:10.1006/anbe.1994.1047

Terborgh J (1983) Five new world primates. A study in comparative ecology. Princeton University Press, Princeton

Waser PM (1976) *Cercocebus albigena*—site attachment, avoidance, and intergroup spacing. Am Nat 110:911–935

Wilson EO (1975) Sociobiology, the new synthesis. Harvard University Press, Cambridge

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Anim Behav 61:1203–1216. doi:10.1006/anbe.2000.1706

Wilson ML, Britton NF, Franks NR (2002) Chimpanzees and the mathematics of battle. P Roy Soc B 269:1107–1112. doi:10.1098/rspb.2001.1926

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168. doi:10.2307/1938423

Wrangham R, 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. doi:10.1163/156853907782512092

Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbors, strangers, and the asymmetric war of attrition. Anim Behav 36:343–347. doi:10.1016/S0003-3472(88)80004-6

Zhang S (1995) Sleeping habits of brown capuchin monkeys (*Cebus paella*) in French Guiana. Am J Primatol 36:327–335. doi:10.1002/ajp.1350360407