

Use of overlap zones among group-living primates: a test of the risk hypothesis

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Summary

Overlap zones between home ranges of neighboring groups of primates are routinely reported to be under-used. However, little is known about how the size of overlap zones varies, or what factors influence their size. Here we use ranging data on three species of group-living primates to test the hypothesis that overlap zones are smaller or used less in species that are subject to a higher risk of lethal aggression in intergroup encounters. Redtail monkeys (*Cercopithecus ascanius*) have a low risk of violence; white-faced capuchins (*Cebus capucinus*) have an intermediate risk; chimpanzees (*Pan troglodytes*) face a high risk of violent encounters with their neighbors. We calculated two indices of use of the overlap zone. First, we assessed the opportunity for groups to meet each other as the range overlap, i.e., the diameter of the home range in relation to the distance between neighboring ranges. Second, we compared the intensity with which groups used the overlap zone by calculating utilization curves that described how space-use patterns change with distance from a group's center of activity. Neither the overlap potentials nor utilization curves supported the risk hypothesis. There was little evidence of differences among the three species, all of which showed substantial under-use of overlap zones. Our data, which provide the first systematic comparison of overlap zones among primates, thus conform to previous reports suggesting that primate groups tend to have large overlap zones, regardless of the risk of violence. Since such zones are potentially responsible for carrying capacity being lower than expected by an ideal-free distribution, it is an important problem to understand why they are apparently widespread.

Keywords: home range, territory, aggression, overlap zone, primate, chimpanzee, redtail monkey, white-faced capuchin, risk hypothesis.

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Introduction

When groups or individuals occupy overlapping home ranges, the areas they share with their neighbors may be used more or less intensely than non-shared areas (over- or under-used, see Figure 1). Variation from over-use to under-use can have important consequences. For instance Kelly (2005) calculated that among Andaman Island hunter-gatherers, under-use of overlap zones reduced the carrying capacity of the habitat by 27% (cf., Keeley, 1996). However in general little is known of the extent of under-use or over-use of overlap zones, or the reasons for variation in overlap. In this paper we test the hypothesis that differences among primate species in the risk of injury during intergroup encounters influence the extent to which social groups use areas of their home range that they share with their neighbors (hereafter ‘overlap zones’).

Theoretically, in a homogeneous environment where foraging effort follows an ideal free distribution, all areas would be used equally. The combined use of overlap zones by all groups sharing the area would be the same as the use of non-overlap areas by a single group. However, no such cases appear to have been reported. While there are occasional accounts of over-use (red howler monkey, *Alouatta seniculus*: Sekulic, 1982), the predominant pattern is for overlap areas to be under-used (e.g., red wood ant *Formica polyctena*, Mabelis (1979); honey ant *Myrmecocystus mimicus*, Holldöbler (1981); black bears *Ursus americanus*, Samson & Huot (2001); wolf *Canis lupus*, Mech (1977), Mech & Harper (2002); tamarins *Saguinus fuscicollis*, *S. imperator*, Terborgh (1983); spider monkeys *Ateles geoffroyi*, Chapman (1990), Shimooka (2005); redtail monkey *Cercopithecus ascanius*, Lambert (1999); chimpanzee *Pan troglodytes*, Stanford (1995), Herbinger et al. (2001); humans, Martin & Szuter (1999), Kelly (2005)).

At least three hypotheses could account for the systematic under-use of overlap zones. First, groups are expected to adjust their ranging behavior to efficiently exploit heterogeneously distributed resources, and may concentrate their foraging effort in areas of particularly high resource density. Overlap zones might, therefore, be under-used because they are areas of resource scarcity (e.g., harvester ants *Pogonomyrmex* spp., Macmahon et al., 2000). Second, a tendency to return to the center of the home range could lead to reduced frequency of range use with increasing distance from the center, entirely independent of any competition with neighbors (e.g., squir-

rels *Tamiasciurus*, Smith, 1968). Third, if hostile interactions with neighboring groups involve a high risk of injury, this could lead to avoidance of overlap areas (Hickerson, 1965, 1970; Mech, 1977; Kelly, 2005). We refer to this as the 'risk' hypothesis. We do not know of any attempts to test among these hypotheses.

Here we assess the 'risk' hypothesis by testing the prediction that a high frequency of serious aggression (i.e., causing wounds or death) during intergroup encounters leads to avoidance of overlap zones. We compare overlap use in three species of primates that vary in their risk of injury during aggressive intergroup interactions. We use a new method of analyzing space use by neighboring groups.

The low-risk species is the redbtail monkey (*Cercopithecus ascanius*). Multiple redbtail populations have been studied, all of which display conspicuous territorial behavior (Cheney, 1987; Cords, 1987). In our Kibale study site, redbtails live in groups of breeding mothers and a single adult male, averaging 25 individuals (Treves, 1998). Kibale groups have long day-ranges (1.5 km) relative to their home range size (0.24 km²), allowing them to defend territories easily (Struhsaker & Leland, 1979; Mitani & Rodman, 1979; Cords, 1987; Lowen & Dunbar, 1994; Lambert, 1999). Areas of overlap between home ranges have been observed at all sites (Cheney, 1987). Intergroup interactions primarily involve calls and brief chases, and no injuries have been reported as a result. Because of the lack of reported injuries from intergroup interactions we consider redbtails a low-risk species.

The medium-risk species is the white-faced capuchin, *Cebus capucinus* (hereafter 'capuchin'). In our Panamanian study site, capuchins live in multimale, multi-female groups of 10–25 individuals (Crofoot, 2007, this issue). Home ranges of capuchin groups averaged 0.80–1.50 km², and overlapped extensively (Crofoot, 2007, this issue). As at other sites, males play a prominent role in intergroup encounters, which are uniformly agonistic, including both high-intensity chases and direct attacks (Rose & Fedigan, 1995; Perry, 1996; Fedigan, 2003; Crofoot, 2007, this issue). In one site, victims of attacks have occasionally been seriously wounded or killed (Gros-Louis et al., 2003). These reports justify capuchins as a medium-risk species.

Although current data suggest that the risk of wounding or death is higher during intergroup aggression among capuchins than redbtails, further data could change the picture. Cases of capuchin wounding and death come from a single site that might prove exceptional. Furthermore, in two congeners

of redtails with similar patterns of territoriality to redtails killing of strange adults has been recorded (*Cercopithecus diana*, McGraw et al., 2002; *C. mitis*, Payne et al., 2003). In *C. mitis* extensive wounding has also been seen in intergroup aggression (Cords, 2002). For these reasons our assignments of low-risk and medium-risk to redtails and capuchins respectively are tentative.

The high-risk species is the chimpanzee (*Pan troglodytes*). Chimpanzee communities occupy territories that are defended by the males in the group. They have a fission–fusion social structure, such that individuals in a community form temporary parties of variable size and composition. When parties from different communities that each have several males encounter one another, interactions tend to involve calls and chases. However when a large party encounters a much smaller party from the neighboring community, a coalition of males is likely to chase, attack and attempt to kill a single victim. Lethal intergroup attacks have been recorded at most long-term study sites, making this a high-risk species (Wilson et al., 2004; Watts et al., 2006; Wrangham et al., 2006).

Given that the probability of an individual being seriously (or fatally) wounded during aggressive intergroup interactions varies among these three species, the risk hypothesis predicts that the overlap zone will be largest for redtails, intermediate for capuchins and smallest for chimpanzees. Similarly the intensity of space use is expected to decrease more steeply with distance from a group's home range center in species with more severe intergroup aggression. Chimpanzees are expected to use overlap zones less intensely than capuchins, and capuchins are expected to use them less intensely than redtails.

These predictions are testable using data on the relative size of overlap zones and the intensity with which they are used among these species.

First, we characterize the relative size of the overlap zone by calculating the proportion of the home range diameter that is overlapped by the home range of a neighboring group (range overlap, R_O). We measure R_O as

$$R_O = (W - D_R) / D_R$$

where W is the diameter of the home range and D_R is the distance between the centers of adjacent groups' home ranges. R_O describes the opportunity for shared use of an overlap zone, rather than how much it is actually shared.

When $R_O < 0$, neighboring groups experience no overlap: they have an unused 'no-man's land' between the edges of their home ranges. This

situation is not expected to occur unless the 'no-man's land' is uninhabitable. When R_O is equal to 0 (i.e., $W = D_R$), home ranges of adjacent groups meet tangentially and there is therefore no overlap zone. This would occur under conditions of extreme territoriality such as a network of hexagonal ranges with complete respect between neighbors. Overlap zones occur when $R_O > 0$. For positive values of R_O , higher values indicate a greater overlap. R_O is expected normally to take values between 0 and 1. When $R_O > 1$, the focal group has no part of its range to which it has exclusive access, and even the center of its range would be visited by at least two neighboring groups. For territorial species this would be an exceptional circumstance.

Second, the intensity with which different species actually use overlap zones can be compared by calculating 'utilization curves' for each species. A utilization curve describes how space-use patterns change with distance from a group's center of activity (i.e., harmonic mean home range center, Dixon & Chapman, 1980). For the three primate species in question, the most central quadrat of a home range was used most intensely, and quadrat use declined towards the periphery of the range. For a given value of R_O , steeper utilization curves translate into less intense use of overlap zones (Figure 2). Accordingly we use ranging data to calculate both R_O and utilization curves. By comparing these variables across species, we test the hypothesis that overlap zones are larger and used more intensely in redtails than capuchins, and in capuchins than in chimpanzees.

Material and methods

Study sites and methods

Lundy and two field assistants observed three habituated groups of redtails with contiguous ranges at Kanyawara in Kibale National Park, Uganda from June to September 2001 (0°13'-0°41'N and 30°19'-30°32'E). Average annual rainfall in Kibale is 1475 mm, with peaks in March-April and September-November (Struhsaker, 1997). Temperature varies from a mean minimum of 12.7°C to a mean maximum of 25.5°C (Struhsaker, 1997). The park includes swamp, grassland and pine plantations, but the observed groups were restricted to primary and regenerating forest. Groups were observed for a total of 138 days and 995 h (Group A: 47 days, 335 h, B: 47 days, 356 h, C: 44 days, 304 h), evenly balanced over daylight hours. The three observers standardized recording methods and tested inter-observer consistency in an

initial phase watching one group. Locations were recorded every 30 min on a 50 × 50 meter grid. A dense network of trails extending over approximately 11 km² facilitated mapping (Lambert, 1999).

Crofoot observed six capuchin groups at the Smithsonian Tropical Research Institute on Barro Colorado Island (BCI), Panama (9°10'N, 79°51'W). BCI is a 15 km² island of semi-deciduous lowland forest that was isolated from the mainland in 1914 by construction of the Panama Canal. The average annual rainfall is 2600 mm/year, 90% of which falls between May and December (Dietrich et al., 1996). Fruit availability correlates with this uneven distribution of rainfall: fruit availability is high during the dry season and into the early wet season, and is lowest during the late wet season (Foster, 1982). It is estimated that 250–300 capuchins, in 15–20 social groups live on BCI (Mitchell, 1989; Crofoot, unpubl. data).

To facilitate finding and following groups, one or two individuals from each group were captured and fitted with radio collars (Crofoot & Lessnau, pers. comm.). Each group was followed 3–6 days per month for a total of >750 direct observation hours. Additionally, from November, 2004–April, 2005, the radio-collared individuals were monitored continuously by a remote system (Automated Radio-Telemetry System, ARTS, M. Wikelski, R. Kays, W. Cochran et al., data not shown). Seven ARTS towers received signals from the radio-collars, allowing the individuals' locations to be triangulated to an accuracy of 50 m. Data presented in this paper come from the ARTS records, i.e., continuous day-light observations every 10 min for 125 days.

Chimpanzees were studied at Kanyawara within Kibale National Park, Uganda, the same site as the redtail study. A single multi-male, multi-female community was observed from 1990 to 2006 by following whatever parties could be found. Data in this paper are from all-day observations (minimum 10 h) in 1998 ($N = 68$ days), 2000 (42 days) and 2002 (90 days), for a total >2000 h. The community averaged about 50 individuals with a home range of approximately 38 km² (Wilson, 2001). Location and party composition data were collected at 15-min intervals by a small team of field assistants. Field assistants were trained by Wrangham, and were normally accompanied in the field by researchers who supervised data accuracy.

Calculating size of overlap zone and intensity of overlap use

For all three species, we used data on the frequency of occupation of grid squares and the density of groups to model the use of overlap zones.

First, we estimated the distance between the centers of the home ranges of neighboring groups. For redbills and capuchins we used field observations, whereas for chimpanzees no field observations were available of the distance between neighbors. We therefore also modeled the distance between the centers of neighboring home ranges (D_R km) using estimates of the density of social groups in the habitat (G groups per km²). Clark & Evans (1954) showed that the expected distance from a group to its nearest neighbor, based on the assumption of maximal (hexagonal) packing, is given by

$$D_R = \sqrt{2/(G * (\sqrt{3}))}$$

This formula appears robust even for randomly distributed populations (Southwood, 1966).

Second we generated an average ‘utilization curve’ for each species that describes how range use varies from the center towards the edge. We defined a group’s home range center by their center of activity, calculated as the harmonic mean of observed locations (Dixon & Chapman, 1980). Chimpanzee and redbill movements were recorded by grid cell, so the center point of each grid cell was used to assign an x , y location to each observation. Home range borders were estimated using minimum convex polygons (100% for chimpanzees and redbills, 95% for capuchins – see Figures 3–5), calculated using the software package Biotas (2004). To accommodate irregularities in range use, we averaged the utilization curves along radii lying north, east, south and west of the center of the home range.

Third, we modeled the occupancy of the overlap zone by two idealized neighbors. For each species, we assigned two groups the same ‘average utilization curve’ (as calculated above). We placed the two curves adjacently on a horizontal axis, with their centers separated by D . We then summed the total range use by both groups in the overlap zone. Figure 1 shows idealized examples.

Results

Overlap potential OP

The risk hypothesis predicts that the relative size of the overlap zones will be highest for redbills, intermediate for capuchins and lowest for chimpanzees. As described above, we assay the relative size of overlap zones by calcu-

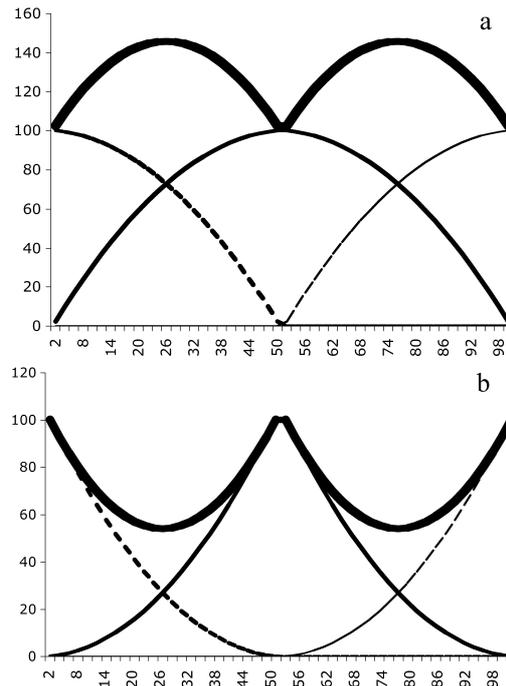


Figure 1. (a) Model of overlap zone: convex utilization curve, $D_R = 0.5 * W$. The figure shows range use along a transect (on the x -axis) running west to east through the center of a model focal group's home range. The center of the focal group's home range is at point 50. Neighboring group are centered at points 0 (western group) and 100 (eastern group). All groups are assigned the same home range size and shape of utilization curve. The thin solid line shows range use by the focal group, from 0 at the peripheries to 100 in the center. Dotted and dashed lines show use of the focal group's range by neighboring groups to west and east respectively. In this example, D_R (the distance between the centers of neighboring ranges) is 50% of W , the width of the home range. Accordingly, the ranges of the neighboring groups meet tangentially in the center of the focal group's range. The thick solid line shows the total use, by all three groups, of each part of the focal group's range. Where neighboring groups have equal use of the range the summed range use is 145% of the intensity of use by the focal group in the center of its range. (b) Model of overlap zone: concave utilization curve, $D_R = 0.5 * W$. Comparison with Figure 1a shows the effect of a concave rather than a convex utilization curve on the use of the overlap zone. Lines and axes as in panel (a).

lating the range overlap, R_O . Table 1 shows the data used to derive R_O and summarizes estimates of R_O .

For redtails, measured distances between centers of home range of the two closest of the three study groups were 0.27 and 0.39 km, yielding a mean of 0.33 km (Figure 3). To assess whether these distances were likely

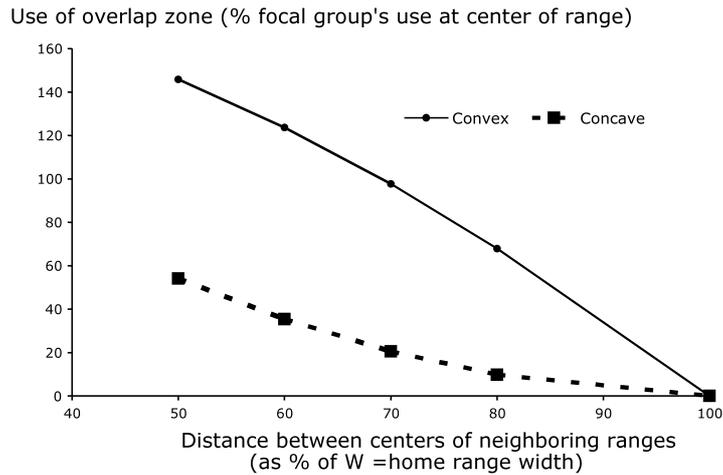


Figure 2. Use of overlap zone as a function of the distance between centers of neighboring ranges. The graph is derived from the model ranges in Figure 1. Lines illustrate the effects of different shapes of utilization curve. As the distance between centers of neighboring ranges increases, the use of the overlap zone falls whether the utilization curve is concave or convex. When the utilization curve is concave, the overlap zone is under-used (less than 100% of the focal group's range use at the center of its range). When the utilization curve is convex, the overlap zone can be over-used provided that D_R , the distance between centers of neighboring ranges, is sufficiently small. We assume that D_R varies between 0.5 and 1.0. For $D_R < 0.5$, neighboring groups on either side of a focal group could meet each other in the center of the focal group's range. For $D_R > 1.0$, a focal group would never meet its neighbors. Neither pattern has been described in our study species.

to have been representative, we compared them with estimates derived by calculating distances between groups based on group density. The average group size of Kanyawara redtails has been reported recently as 25 (Treves, 1998), with a population density of 70–158 per km² (Struhsaker, 1997). This yields estimates of group density between 2.8 and 6.3 per km². Our study occurred in an area of relatively high density, suggesting that the figure of 6.3 per km² is more appropriate. An even distribution of groups is indicated by the fact that two of the study groups had four known neighbors, while the third, which lived on the forest edge, had two neighbors. Assuming a hexagonal packing of groups and a group density of 6.3 per km², expected D_R would be 0.43 km (Clark & Evans, 1954). This means that the observed distance between the closest centers of neighboring ranges (0.33 km) was 22.9% lower than the expected (0.43 km). To be conservative, we, therefore, use both our observed and expected distance (0.33 km, 0.43

Table 1. Range use data. D_R = distance in km between centers of closest neighboring home ranges. Derivation of data is explained in text.

	Redtail monkey	White-faced capuchin	Chimpanzee
D_R (km) (observed) (range)	0.33 (0.27–0.39)	0.84 (0.36–1.20)	–
Group density (per sq km). Ranges of estimates shown in brackets	(2.8–) 6.3	1.16 (1.0–1.3)	0.019–0.038
D_R (km) by calculation from group density	0.43 (-0.64)	1.00	5.5–7.8
Home range size (sq km)	0.21	0.91–1.61	38
W (km) (diameter of home range, assuming it is circular)	0.52	1.08–1.43	7.0
Range overlap, $R_O = (W - D_R)/D_R$ (using observed D_R)	0.58	0.29–0.70	–
Range overlap, $R_O = (W - D_R)/D_R$ (using D_R modeled from group density)	0.21	0.08–0.43	–0.10–0.27

km respectively) to estimate the degree of overlap between nearest neighbors.

Redtail home range sizes in this study based on grid cell counts were 0.16, 0.23 and 0.25 km² for the three groups (mean 0.21 km²), close to the previously reported mean of 0.24 km² (Struhsaker & Leland, 1979). The diameter (W) of an idealized circular home range of 0.21 km² would be 0.52 km. Accordingly for $D_R = 0.33$, R_O , the range overlap, = 0.58 (i.e., $(W - D_R)/D_R$; Table 1). For $D_R = 0.43$, $R_O = 0.21$.

For capuchins, measured distances between centers of home range for the six study groups were assessed for eight cases where a given group was clearly the nearest neighbor (see Figure 4), yielding an average D_R of 0.84 km (range 0.36–1.20, standard deviation 0.25). As with redtails, we compared the observed value of D_R with an expected value derived from group density. Capuchin group density was estimated at 1.16 per km², given that 15–20 groups are estimated to occur in 15 km² (Mitchell, 1989; Crofoot, unpubl. data). Spatial distribution of neighbors is illustrated in Figure 4, suggesting an even distribution. Accordingly the estimated group density predicts a D_R of 1.00 km (Clark & Evans, 1954). As with redtails, the observed D_R is lower than the expected D_R based on group density (15.8% lower). Again, therefore, we use both our observed and expected distance

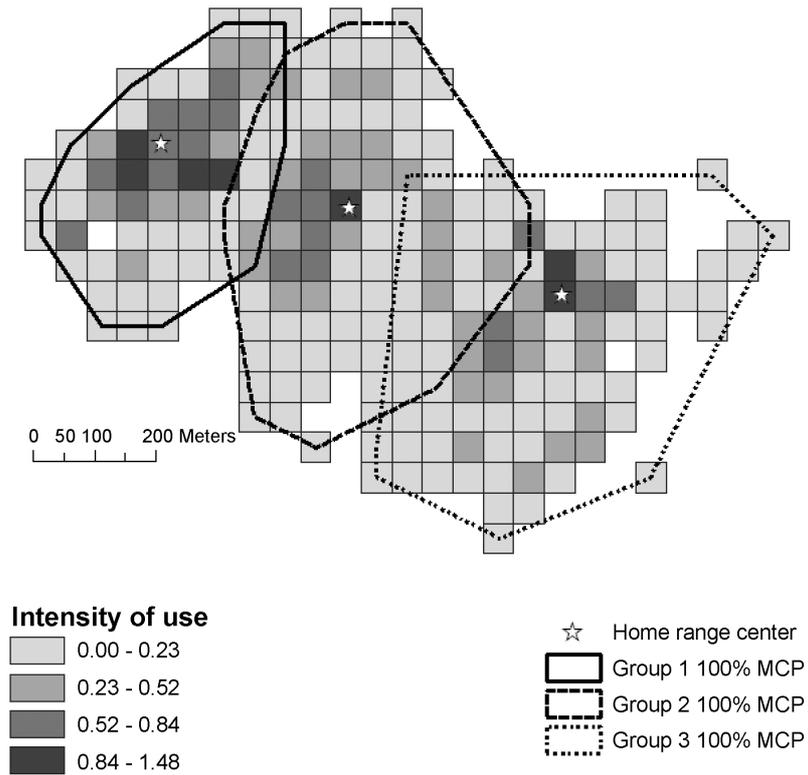


Figure 3. Home ranges of redbtail monkeys. Ranges of three adjacent groups are shown. Outlines show minimum convex polygons containing 100% of observations. Stars show centers of range use. Intensity of use is indicated by depth of black. Note that in areas of overlap between groups, total use is less than in central areas of the home range. Grid squares have sides of 50 m.

(0.84 km, 1.00 km respectively) to estimate the degree of overlap between nearest neighbors.

Capuchin home ranges on BCI were reported as 0.91–1.61 km² (Crofoot, 2007, this issue), yielding W of 1.08–1.43 km (calculation as for redbtails, above). Assuming $D_R = 0.84$ km, R_O for capuchins is therefore 0.29–0.70; for $D_R = 1.00$ km, R_O for capuchins is 0.08–0.43.

Distances between neighboring chimpanzee ranges were not observed directly. To estimate the distance, we calculated the density of chimpanzee groups from data on population density and group (community) size. Population density for Kibale National Park has been estimated by nest-count census at approximately 1429 individuals in 760 km², i.e., 1.9 individu-

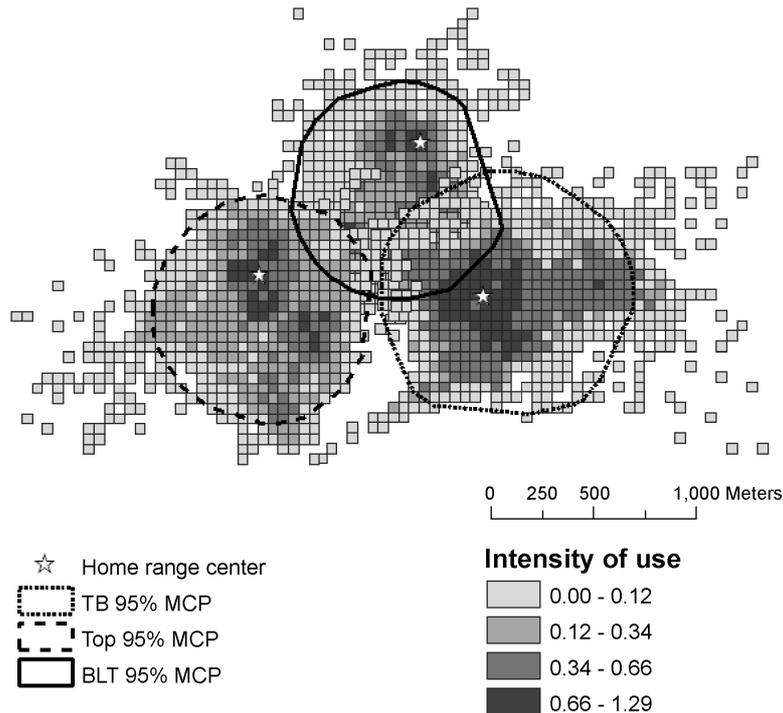


Figure 4. Home ranges of white-faced capuchins. Ranges of three adjacent groups are illustrated. Format is same as Figure 3. Grid squares have sides of 50 m.

als per km² (A. Plumptre, pers. comm.). The focal community size was 50. In Kibale two other habituated communities have been estimated as >100 (Kanyanchu) and 150 individuals (Ngogo) (J. Lloyd, pers. comm.; Watts, 2004). However, Kanyanchu and Ngogo communities are unlikely to be representative of the average size in Kibale because they occupy an especially productive area and are the largest chimpanzee communities ever described. Using an average group size of 50–100, we estimate group density as 0.019–0.038 per km². The study community was bordered by chimpanzees suggesting one community each to north, east, south and west, i.e., an even distribution of neighbors. Accordingly the group density estimates give an expected $D_R = 5.5\text{--}7.8$ km (Clark & Evans, 1954).

Using the home range estimate for our study community of 38 km² (Wilson, 2001), $W = 7.0$ km. Assuming $D_R = 5.5\text{--}7.8$ km, R_O for chimpanzees is $-0.10\text{--}0.27$. This seems likely to be an over-estimate, however, given that the observed D_R for redtails and capuchins were reduced by 22.9% and

16.2% respectively compared to the expected values. If a similar difference occurred for chimpanzees, the estimate for D_R would become 4.2–6.5 km and R_O for chimpanzees would be 0.08–0.67.

Estimated values of R_O thus have wide ranges, much overlap and no obvious trend (Table 1). The estimates for capuchins include those for both redtails and chimpanzees (Table 1). We have low confidence in our estimate for chimpanzees, given that D_R was not observed directly and that average group size is unknown. While our data are compatible with the prediction that R_O is highest for redtails, intermediate for capuchins and lowest for chimpanzees, they do not directly support it.

Utilization curves

Utilization curves for the three species were calculated by averaging, for each home range, frequency of grid cell use (as a percentage of the maximum use at the center of the home range) from the center to the northern, eastern, southern and western edges of the range. Data were averages of three groups for redtails, three groups for capuchins and three years for chimpanzees (Figures 3, 4 and 5).

Results are shown in Figure 6. All curves are concave, and indicate that overlap zones were under-used in all three species (cf. Figure 2).

No species differences are clear. Although the chimpanzee curve appears more concave, suggesting greater avoidance of the overlap zone, utilization curves for individual groups and years showed large overlap with each other, obscuring any potential species differences.

To examine the extent of avoidance of the overlap zone, we combined the observed utilization curve with an assumed value for range overlap of $R_O = 0.33$. Figure 7a shows a sample result for redtail monkeys indicating that in the overlap zone, the total use by both groups amounts to less than 20% of the use by focal groups of the center of their ranges. Capuchins and chimpanzees gave similar results.

The estimated use of the overlap zone is influenced by the value of R_O , which was subject to large potential error (see Table 1). We therefore considered how the overlap zone was utilized when $R_O = 1.0$. A value of $R_O = 1.0$ means that the overlap is so large that two groups from opposite sides of a focal group may meet each other in the middle of the focal group's range, a phenomenon that appears not to have been reported for any of our species

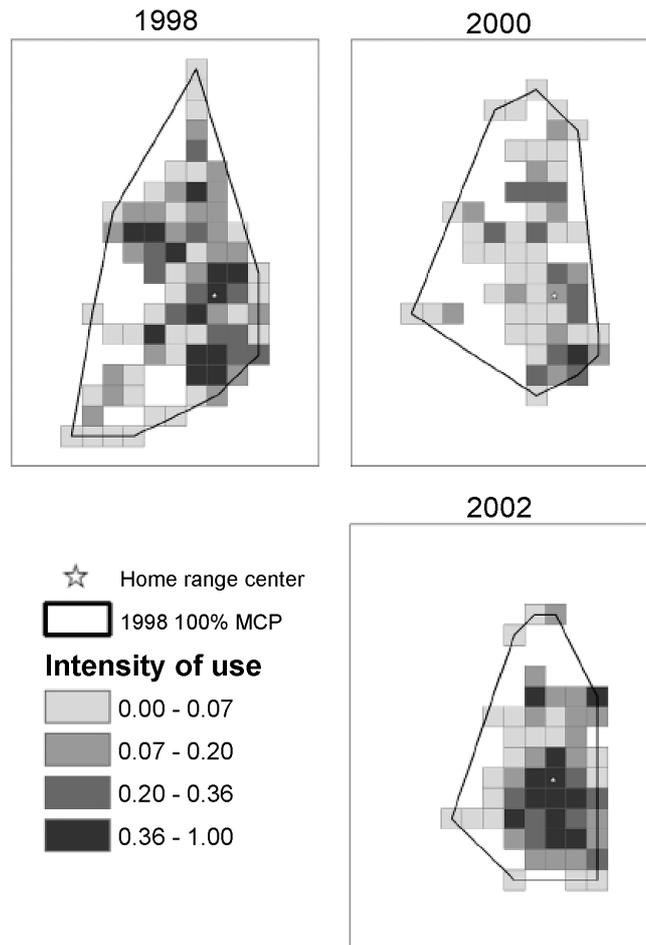


Figure 5. Home range of chimpanzees. The home range of the study community is shown for three years. Format as in Figure 3. Grid squares have sides of 500 m.

(e.g., Struhsaker & Leland, 1988). Even with this high degree of range overlap, however, the modeled use of the overlap zone remains less than 30% of the use at the center of the range (Figure 7b).

Discussion

Our data represent the first attempt to test the ‘risk hypothesis’, which states that species subject to greater risks from aggression with their neighbors have narrower and/or less intensely used overlap zones. The hypothesis predicts

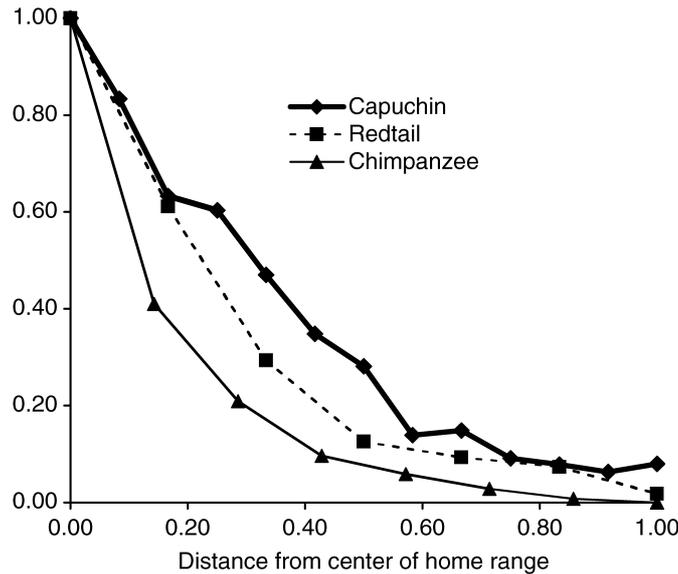


Figure 6. Normalized utilization curves of range use. Curves show the decline in frequency of grid cell occupation from the center of the home range to the outer edge. 'Distance from center of home range' is a proportion of the distance to the edge of the home range (i.e., $0.5 * W$, the calculated radius of a circular home range (Table 1): redtail: 0.30 km, rounded up from 0.27 km; capuchin: 0.6 km; chimpanzee: 3.5 km). 'Frequency of grid cell use' is proportional to the frequency of use at the center of the home range. Curves are averages of four cardinal directions from center of home range. Samples: redtail, 3 groups; capuchin, 2 groups; chimpanzee, 1 group, 3 years.

that R_O , the range overlap as indexed by the diameter of the home range relative to the distance between centers of neighboring groups, will be smaller in more vulnerable species; and/or that the rate at which grid use declines from the center of the range will be steeper in more vulnerable species. Neither prediction was consistently supported. Estimates of range overlap (R_O) overlapped across the three species and could not be confidently ranked. As predicted, chimpanzees showed a steeper utilization curve than other species. However, redtails had steeper utilization curves than capuchins, in contrast to expectation. Our data therefore do not support the risk hypothesis.

Some of the variables on which this analysis rests are subject to error variance, and our data comes from studies that used different methods and schedules of observation. For example, the time depth varied from one season to multiple years, and the number of groups under observation varied from one to six. Such differences could lead to various problems. Thus, if neighbor-

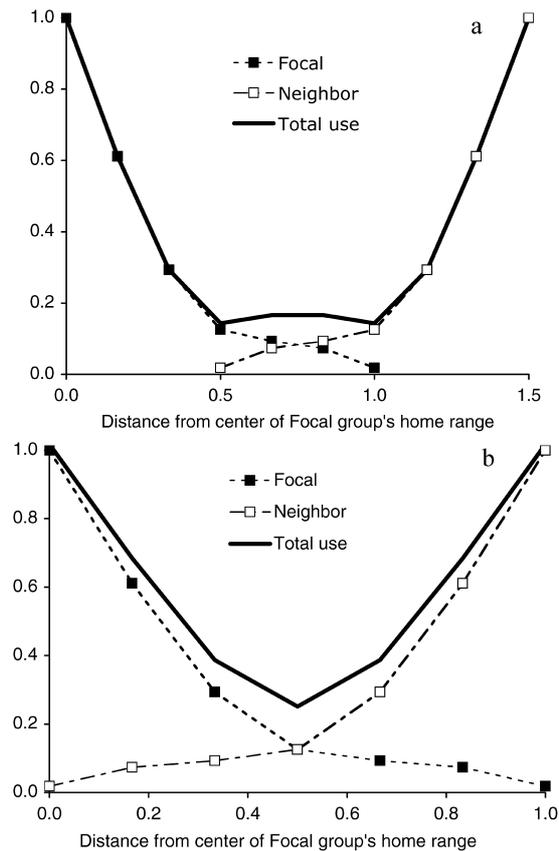


Figure 7. (a) Schematized use by redtails of overlap zone, based on field data. Curves show the frequency of grid cell use of home range by a focal group and one neighboring group along the line joining the centers of the two ranges. The utilization curve for the focal group (largely masked by the 'Total use' curve) is the same as in Figure 6. The utilization curve for the neighboring group ('Neighbor') is the mirror image of the focal group's utilization curve. The center of the neighbor's utilization curve is located at a distance of 1.5 home range radii from the center of the focal group's home range. The distance of 1.5 home range radii is derived from redtail data in Table 1 (i.e., D_R , the distance between centers of neighboring home ranges, = $0.75 * W$, the diameter of the home range). The graph shows that the summed use of the overlap zone by two neighboring groups is small, less than 20% of the use at the center of the home range. (b) Schematized use by redtails of overlap zone, based on maximum likely overlap. The graph is as in panel (a), except that the center of the Neighbor's utilization curve is located at a distance of 1 home range radius from the center of the Focal group's home range. This distance is chosen to represent an exceptionally high degree of overlap, more than has been reported in redtail monkeys (given that it implies that a group's western and eastern neighbors may occasionally meet inside the focal group's range). Panel (b) shows that the summed use of the overlap zone is still small (less than 30%) even when there is a high degree of overlap.

ing groups used an overlap zone alternately by season, studies of longer duration could in theory cause the intensity of overlap to be over-estimated. Again, our estimates for overlap among chimpanzee groups depended on inferring the distance between the center of neighboring group ranges based on group density. Furthermore, while we assumed for comparative purposes that home ranges were circular, it is possible that differences in the shape of home ranges reduce the comparability across species. For such reasons our conclusions are preliminary. Nevertheless, in all three species range use estimates came from >1000 h of data and were based on observations spread evenly across daylight hours. In all species the estimated values of R_O were similar, and the utilization curves were so steep that the extent of overlap was relatively insensitive to the value of R_O .

The uniformity of these patterns suggests they may be widespread in primates, i.e., that there tends to be substantial under-use of overlap zones. This conclusion has been suggested previously based on individual studies. For example, Boesch & Boesch-Achermann (2000) found that among chimpanzees 75% of time was spent in the central 35% of the range. While chimpanzees are a high-risk species, the territorial agile gibbon (*Hylobates agilis*) is not, since no deaths have been reported in intergroup aggression. Yet a group used its overlap regions only one third as much as expected (Gittins, 1980, 1982).

Under-use and over-use are relative terms of course. In our analysis we assessed frequency of grid cell use as a percentage of use in the center of the range. Even if resource distribution was homogeneous, however, our data are inadequate to show that the peripheral areas were under-used with respect to resources. Rate of resource extraction is not necessarily correlated with frequency of grid cell use; the center of the range could in theory have been over-used (e.g., unsustainable rate of prey removal); and it is possible that overlap zones were areas of low resource abundance. Nevertheless our results clearly raise the possibility that overlap zones have low rates of resource extraction. They could therefore be locations of high prey density (e.g., Stanford, 1995). These could be important by providing opportunities for some individuals, such as solitaries of either sex, to center their foraging effort in overlap zones rather than living in ordinary groups (e.g., Williams et al., 2002).

Our results offer a clear suggestion for why the risk hypothesis was rejected. They indicate that the overlap zone was substantially under-used not

only in the most vulnerable species (chimpanzees) but also in capuchins and redtails. This means that the failure of the risk hypothesis was due to under-use by species that experience a relatively low risk of injury in intergroup aggression, rather than to over-use by vulnerable species.

In conclusion, we suggest that it may be common for overlap zones among primates to be severely under-used, and that further comparative analysis is worthwhile to examine this idea. If under-use proves as extensive as in our data, it will be important to find out why. In some cases, groups doubtless modify their ranging behavior to allow them to avoid areas of low resource density. In others, groups could in theory spend little time in border areas in order to minimize the costs of returning to a preferred center. Tests among such ideas will suggest why there is such a substantial under-use of the environment by species that differ widely in social system, body mass and territorial style.

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