



## Food and range defence in group-living primates

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Why do some primate groups contest access to food resources primarily at territorial borders (periphery defence), whereas others are more likely to contest resources in the centre of the home range (core defence)? One possibility is that central areas contain more food resources and so are more important for core-defending groups, whereas peripheral areas are more valuable for groups that defend territorial boundaries. I tested this hypothesis by analysing the distribution of resources in home ranges and aggressive intergroup interactions for six groups of grey-cheeked mangabeys, *Lophocebus albigena*, and six groups of redbtail monkeys, *Cercopithecus ascanius*, at the Ngogo site in Kibale National Park, Uganda. Neither mangabeys nor redbtails exhibited core or boundary defence in this study; instead, both species appeared to defend discrete feeding sites, and neither the core nor peripheral home range areas consistently contained greater quantities of food. I also compared variables that are frequently used to characterize primate food availability (the feeding value of the interaction site versus food abundance, distribution and patch size) to determine if they are equally accurate in predicting aggressive food defence. Whereas site feeding intensity predicted aggression by redbtails, aggression by mangabey males correlated with the abundance and distribution of resources. These results demonstrate the importance of testing multiple aspects of food availability, which can vary in importance among different primate populations. I conclude by proposing a new model of food and range defence in group-living primates that predicts specific relationships between various food characteristics and core, patch and periphery defence.

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Many animal species defend food resources during intergroup interactions (IGIs), but the way in which food defence is expressed varies among species and even among populations of the same species (Waser & Wiley 1979; Ostfeld 1985; Lott 1991; Oberski & Wilson 1991), particularly among primates (Cheney 1983). Despite the fact that aggressive intergroup competition for food has important effects on group access to feeding sites (Putland & Goldizen 1998; Mertl-Millhollen et al. 2003; Harris 2006; Mitani et al. 2010), within-group social relations (Radford 2008; Puurtinen & Mappes 2009) and the fitness of group members (Robinson 1988), it is still unclear exactly which factors give rise to different patterns of resource defence.

In some food-defending populations, groups interact aggressively in the periphery of the home range, whereas in others, groups interact throughout their ranges (Cheney 1983; Giraldeau & Ydenberg 1987). Typically, patterns of aggression and contest outcome covary with the location of the interaction. In populations

where groups interact primarily at range edges, resident groups are highly aggressive towards, and successfully evict, neighbours who have intruded into their range, but are less aggressive and are often evicted when they intrude into the ranges of their neighbours (this pattern is hereafter referred to as 'periphery defence'; Hinde 1956; Pride et al. 2006). In populations where groups interact throughout their ranges, the intensity of aggression and the likelihood of displacing a neighbour is higher in the core than in the periphery of the range ('core defence'; Waser & Wiley 1979; Crofoot et al. 2008). These labels do not imply that a group defends only the outer or inner areas of its range. In a periphery defence system, IGIs are simply more likely to occur in the periphery; in core defence, the label refers to the group's greater success in evicting intruders from the core of its range.

What causes some populations to exhibit periphery defence, and others core defence? Both forms of defence are exhibited by groups living in economically defensible home ranges (that is, where the D index > 1, meaning daily travel distance exceeds home range diameter for maximum effectiveness in detecting and evicting intruders; Mitani & Rodman 1979; Kinnaird 1992). One possibility is that core defence corresponds with a certain range of D index values, and periphery defence with a different range of

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values. Unfortunately, insufficient data are available to test this idea. Alternatively, patterns of relative food availability in core versus peripheral areas may give rise to particular forms of defence. A few studies have noted that in periphery-defending populations, contested resources are located near home range edges (Garber 1988; Wilson et al. 2012), and in core-defending populations, core areas contain more food per unit area than peripheral areas (Harris 2006; Kinnaird 1990).

Measuring the spatiotemporal patterns of food availability (and doing so from the perspective of the consumer, rather than from a purely botanical perspective) is a particularly challenging task for primates, because their foods tend to be highly variable in density, distribution and quality (Vogel & Janson 2011). For this reason, several authors have approached the issue by tracking the feeding patterns of their study groups and assigning a value to each IGI location based on the percentage of feeding records occurring at that site (Fashing 2001; Sicotte & MacIntosh 2004; Korstjens et al. 2005; Harris 2010). However, this approach does not necessarily correspond with the conditions under which feeding sites are hypothesized to be economically defensible (i.e. when access to food limits reproductive success and feeding sites are monopolizable by groups; Brown 1964). Primate groups are expected to defend feeding sites when the overall abundance of food in the home range is low, because this is when individual reproduction is most likely to be food-limited (van Schaik 1989; Isbell 1991). Additionally, groups are expected to defend monopolizable, patchily distributed resources large enough to feed all or most group members, because this is when individuals are most likely to be motivated to participate in collective defence (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). No tests have been conducted to determine whether site feeding intensity is a reasonable substitute for food abundance, feeding site distribution and food patch size, and whether all of these variables are equally useful for predicting the occurrence of food defence.

The first objective of this study was to test the hypothesis ( $H_1$ ) that core and periphery defence arise from differences in the abundance of food in core versus peripheral areas. I observed six groups of redtail monkeys, *Cercopithecus ascanius*, and six groups of grey-cheeked mangabeys, *Lophocebus albigena*, at the Ngogo field site in Kibale Forest, Uganda. Previous studies of redtails in this forest described intergroup relations as territorial (Struhsaker & Leland 1979), although the basis for this label is unclear. Anecdotal reports indicate that mangabeys do not exhibit periphery defence but do exhibit aggressive IGIs at large fruit trees (T. Windfelder & J. Lwanga, personal communication) and so by default, I expected that they would exhibit core defence. Thus I predicted the basal area of food stems to be higher (per unit area) in core areas than in peripheral areas for mangabeys, and the reverse for redtails ( $P_1$ ). I also predicted that mangabey groups would be aggressive in core areas more often than in peripheral areas, and the reverse for redtail groups (largely because intergroup interactions should occur primarily in peripheral areas;  $P_2$ ).

The second objective was to test the hypothesis ( $H_2$ ) that site feeding intensity is a reasonable proxy for overall food abundance, feeding site distribution and food patch size. Thus, I predicted that both mangabey and redtail groups would be more aggressive in sites of high feeding intensity and when overall food abundance was low, feeding sites were patchily distributed and food patches were large ( $P_3$ ).

## METHODS

### Study Site and Species

I conducted this study at the Ngogo research site in Kibale National Park, Uganda, which consists of old-growth, moist evergreen

forest, interspersed with small areas of colonizing forest and riparian habitat (Struhsaker 1997). I worked with a team of nine field assistants to follow the mangabeys and redtails for 5–15 months per group (Table 1) from January 2008 to the end of March 2009.

Both mangabeys and redtails are female-philopatric, but whereas redtail groups contain only one adult male, mangabey groups are typically multi-male (Struhsaker & Leland 1979). The diets of the two species exhibit a high degree of overlap at Ngogo: when considering species that account for  $\geq 1\%$  of the annual plant diet, mangabeys consume 19 species and redtails 18 species; 11 plant species are important foods for both redtails and mangabeys (Brown 2011). Fruits make up 79% of the plant diet for each species. Mangabey home ranges are much larger than redtail ranges (mean  $\pm$  SE =  $1.68 \pm 0.11$  km<sup>2</sup>,  $N = 6$  groups, versus  $0.38 \pm 0.03$  km<sup>2</sup>,  $N = 6$ ), and within each species, ranges of neighbouring groups overlap extensively (overlap per pair of mangabey groups:  $0.43 \pm 0.11$  km<sup>2</sup>,  $N = 13$  dyads; redtails:  $0.10 \pm 0.03$  km<sup>2</sup>,  $N = 11$ ), providing many opportunities for intergroup interaction. Despite differing range sizes, the two species travel nearly the same distance per day (mangabeys:  $1.43 \pm 0.27$  km per 11 h day,  $N = 215$  group-days; redtails:  $1.40 \pm 0.32$  km,  $N = 92$ ); as a result, redtail groups use a greater proportion of their home ranges per week than the mangabey groups.

On each observation day, two assistants followed each group, recording data from 0730 hours to 1830 hours. I moved among groups, monitoring and assisting with data collection. We estimated the location of each study group's centre-of-mass at 30 min intervals using a  $50 \times 50$  m gridded map of the trail system, and by pacing between trails. We also conducted group-wide scan samples at 30 min intervals, in which we walked through the group and recorded the activity of 50% of the adults and subadults, watching each animal for five seconds and then recording its activity on the sixth second. If the animal was foraging for or ingesting plant parts, we recorded its activity as 'feeding' and noted the part eaten, species, location and diameter at breast height (DBH) of the tree or liana.

### Intergroup Interactions

An IGI began when we estimated the nearest edges of two groups to be separated by  $\leq 50$  m (redtails) or  $\leq 100$  m (mangabeys), regardless of whether either group exhibited aggression, and

**Table 1**

The number of intergroup interactions (IGIs) in which each mangabey and redtail group was observed as a focal group (including IGIs with nonstudy groups), the number of adults and subadults in each group, the number of observation hours per group, the number of months across which the observations were distributed and the total number of location estimates used to calculate the home range of each group

Species	Group	No. IGIs*	Group size†	Observations		Centre-of-mass location points
				Hours	Months	
Mangabeys	M1	10/4	13–14	2023	15	3973
	M2	9/5	16–19	1735	15	3451
	M3	7/7	12	2015	15	3850
	M4	1/2	2–3	487	10	911
	M5	1/4	10–11	1429	10	2759
	M6	4/6	15–16	780	5	1541
Redtails	R1	46	12–13	1034	12	1946
	R2	52	10–11	938	12	1775
	R3	27	10–11	919	12	1676
	R4	0‡	10	269	6	758
	R5	6	15	576	5	1207
	R6	1	18	558	5	1161

\* The numbers before and after the slash indicate the number of mangabey whole group and subgroup IGIs, respectively.

† 'Group size' is given as a range because adult and subadult males sometimes joined or left the focal groups.

‡ The R4 group participated in IGIs as an opposing group, but not as a focal group.

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