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Food and range defence in group-living primates

Michelle Brown[a,b,*]

[a] Department of Anthropology, University of New Mexico, Albuquerque, NM, U.S.A.
[b] Anthropologisches Institut und Museum, Universität Zürich, Switzerland

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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 redtail monkeys, *Cercopithecus ascanius*, at the Ngogo site in Kibale National Park, Uganda. Neither mangabeys nor redtails 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 redtails, 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.

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

* Correspondence: M. Brown, MSC01-1040, Anthropology, 500 University Blvd NE, University of New Mexico, Albuquerque, NM 87131, U.S.A.
E-mail address: moowalks@gmail.com.

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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^2, N = 6 groups, versus 0.38 $\pm$ 0.03 km^2, N = 6), and within each species, ranges of neighbouring groups overlap extensively (overlap per pair of mangabey groups: 0.43 $\pm$ 0.11 km^2, N = 13 dyads; redtails: 0.10 $\pm$ 0.03 km^2, 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.

ended when the groups were separated by distances greater than these thresholds. The thresholds were based on the typical distance at which individuals appeared to be able to see the opposing group and began to react to its presence (i.e. by staring, producing alarm or aggressive vocalizations, and lunging at, chasing or physically attacking members of the other group), which differed between the two study species. Although the mangabey threshold distance was greater than the redtail distance, individuals of different mangabey groups were generally less than 50 m apart during IGIs; in other words, although IGIs began at greater distances, the groups inevitably interacted at much closer range. When a pair of groups met more than once on a given day, I used only the first interaction in the analyses. I did not include interactions with lone males (which occurred infrequently) in the analyses, and for interactions in which we were following both groups, I used data from only one group.

Males and females may be motivated to participate aggressively in IGIs by different factors; thus the behaviour of each sex must be treated separately (Harris 2007). Both mangabey and redtail females are expected to exhibit food defence, because they consume patchily distributed fruits and are philopatric (Struhsaker & Leland 1979; Wrangham 1980; Sterck et al. 1997). Male mangabeys, but not male redtails, are expected to defend food resources during IGIs, because mangabey females are reproductively monopolizable (owing to oestrous asynchrony) and redtail females are not (owing to a combination of oestrous synchrony and frequent copulations with extra-group males during mating seasons; Fashing 2001). Immediately following an IGI, the observers recorded the location of the IGI and whether any individual of either sex had chased or physically contacted a member of the opposing group on a standardized check-sheet.

Mangabeys exhibited two distinct types of IGI, which I analysed separately. In 'whole-group IGIs' the centres-of-mass of the two groups were <100 m apart and most individuals of one group appeared to be able to see most individuals of the other group. In 'subgroup IGIs' the centres-of-mass of the two groups were >200 m apart and only one or a few individuals of one group appeared to be able to see members of the opposing group. Subgroup IGIs were the result of one or a few individuals (always males, and females joined them in a few instances) distancing themselves from their group mates and rapidly approaching a neighbouring group. A subgroup was typically several hundred metres away from the rest of its group, and out of visual contact. While the subgroup approached the neighbour, the remainder of its group remained in place or ran away. Redtails exhibited only whole-group IGIs.

Data Analysis

I identified the core and periphery of each home range in Biotas (Ecological Software Solutions LLC, Hegymagas, Hungary) using group centre-of-mass locations recorded during the half-hourly group scans (Table 1). I chose to base the core and periphery on centre-of-mass locations, rather than feeding locations, because the latter were highly influenced by fruiting irregularities during the 2008–2009 study period (M. Brown, personal observations) and the short duration of observations for some groups. I calculated the core and periphery of each range as the 50% and 95% kernel density polygons, using the mean squares function, to ensure that the outer polygons were single, contiguous polygons with no bubbles of unused space. Although there were substantially fewer location points for a few of the study groups than for others (Table 1), data accumulation curves indicated that the home range size for each group reached an asymptote, indicating that each group's range was adequately sampled.

I evaluated 235 50 x 50 m botanical plots in which we measured the DBH of all stems at least 10 cm ($\geq$1 cm for lianas) of each important food species (i.e. those constituting $\geq$1% of the annual diet). We sampled $\geq$10% of each mangabey home range area and $\geq$20% of each redtail area (Table 2). For each home range, I calculated the mean basal area of food stems per plot in the core and peripheral areas and log transformed the data to achieve a normal distribution. To evaluate temporal variation in food availability per area, I also calculated the mean food-bearing basal area per plot, per observation period: this was the basal area of a species in a plot, times the percentage of quadrats with food (i.e. the number of quadrats in which groups fed on that plant species during that observation period divided by the total number of quadrats in which all groups were observed to feed on that species during the study period), summed across food species.

During IGIs, the dependent variable of interest was whether any female or male from the focal groups exhibited behaviours consistent with food defence, so I scored male and female intense aggression as either present or absent. Intense aggression consisted of chases and/or physical attacks on a member of the opposing group.

I calculated 'food abundance' as the summed availability of fruits, flowers and leaves in a given observation period, based on the subjects' feeding behaviour. The availability of each food species was the product of its stem density, stem size (basal area) and a proxy of the percentage of food-bearing stems (the percentage of quadrats with food). I scored stem density as the mean number of stems per botanical plot; for species with densities <1 stem/quadrat, I substituted a value of 1 because abundance was assessed only for feeding quadrats in which the monkeys fed during that observation period (i.e. where there must have been at least one stem). Basal area (DBH converted to area) was the mean basal area of trees in which redtails and mangabeys fed; I log transformed this variable because the value spanned multiple orders of magnitude. Lastly, it was necessary to take into account the fact that not all stems of a species bear fruit or flowers simultaneously, but concurrent phenological censuses were unable to accurately estimate the percentage of food-bearing stems (Brown 2011). Instead of using phenological data, I determined the percentage of food-bearing quadrats for a particular plant species: I calculated this as the number of quadrats in which groups were observed to feed on that species in the observation period divided by the total number of quadrats in which all groups were observed eating that species throughout the entire study.

I calculated 'feeding site distribution' as the variance-to-mean ratio of the distances among a group's feeding quadrats during an observation period. This method is more appropriate than calculating the weighted mean distribution of each food species consumed during the observation period (using, for example, the Morisita index; Morisita 1959), because not all stems of a species produce food at the same time, and not all food-bearing stems are utilized by a group (M. Brown, personal observations). Furthermore, as my team and I only recorded the activities of half of the adults and subadults in the group during scans, using the entire quadrat as the unit of measure accommodated the likelihood that multiple stems (of different species) were fed upon within a single quadrat. Ratios <1 indicated uniform distributions and ratios >1 patchy distributions.

Overall food abundance and feeding site distribution were significantly correlated for mangabeys (pairwise correlation: $R = -0.648$, $N = 37$ group-periods, $P < 0.001$) and redtails ($R = -0.609$, $N = 46$ group-periods, $P < 0.001$). I created a composite of the two variables ('food abundance-distribution') by first subtracting 1 from each distribution value (so that uniform distributions had negative values, zero indicated a random distribution and patchy distributions were positive), then multiplied the adjusted distribution value by the abundance score.

I calculated ‘food patch size’ as the weighted average basal area of the food trees in the general IGI location (i.e. the quadrat containing the focal group’s centre-of-mass at the start of the IGI, as well as the surrounding two layers of quadrats, to yield a radius of approximately 125 m around the group centre). As we recorded feeding for only half of the group’s adult and subadult members during each scan, I accounted for the likelihood that additional trees of each food species were utilized by other group members during and between scans by multiplying the basal area for each food tree by the species’ stem density per quadrat. I then weighted this figure by the number of feeding records for each species because some foods were fed upon more intensively than others, and I assumed that larger patches resulted in more feeding records. I divided the resulting number by 1000 so that the regression results (odds ratio and SE) would be easily interpretable.

‘Site feeding value’ was the percentage of the focal group’s feeding records during the observation period that occurred within the IGI location (i.e. the quadrat containing the group’s centre-of-mass at the start of the IGI, as well as the surrounding two layers of quadrats).

Statistical Analyses

To determine whether core and peripheral areas contained significantly different quantities of food, I used *t* tests to compare the mean basal area of food stems per quadrat, and multilevel regression models to compare the basal area of food-bearing stems per quadrat, per observation period. The fixed effects in the multilevel models were home range area (core or periphery), group identity and an interaction between these two main effects; the random effects were quadrat identity and observation period, and were crossed rather than nested because each quadrat was sampled in multiple observation periods (Rabe-Hesketh & Skrondal 2008). The absolute basal area was normally distributed, but the basal area of food-bearing stems per observation period was not, so I log transformed the latter.

I used one-sample proportion tests to determine whether the frequency of IGIs was higher in one home range area than another, based on the percentage of time spent in that area. I used logistic multilevel models, with group identity and observation period as crossed random effects, to evaluate whether sex-specific aggression was more likely to occur in core versus peripheral areas. The male and female models for this analysis included IGI location (core versus periphery) and resource heterogeneity (food-bearing basal area in the core was equal to, greater than or less than the food-bearing basal area in the periphery) as fixed effects. For mangabeys, I also included IGI type (whole group or subgroup).

To evaluate whether any of the food variables predicted sex-specific aggression, I used logistic multilevel models (with group identity and observation period as crossed random effects). This set of male and female models included site feeding intensity, food abundance-distribution and patch size as fixed effects. A logistic regression with power = 80%, $\alpha = 0.05$, a medium effect size (odds ratio = 2.19; Cohen 1988), no collinearity among the fixed effects, and a 27% incidence of 1 s or 0 s (i.e. the approximate frequency of mangabey female aggression or male nonaggression) requires 79 IGIs (Faul et al. 2009). As the number of mangabey IGIs was well below this minimum sample size, I repeated the mangabey analyses using nonparametric Wilcoxon two-sample tests to determine whether a more conservative analysis would yield the same pattern of results. Based on the results relating to P_3, I also conducted a post hoc test to determine whether mangabey groups had more high-intensity feeding quadrats available to them, per observation period, than the redtail groups and whether the number of such quadrats varied across periods of high and low abundance. For this analysis, I calculated the number of feeding quadrats per group, per observation period, that were high-intensity quadrats (>1 SD above the mean quadrat feeding value). I then used a linear mixed model to determine whether the number of high-intensity feeding quadrats varied as a result of overall food abundance and between monkey species (with an interaction term between abundance and monkey species, and with group identity and observation period as random effects). I log transformed food abundance and square-root transformed the number of high-intensity feeding quadrats to achieve normal distributions.

I used linear multilevel models to determine whether the four food variables were correlated, and to determine whether each variable differed significantly among redtail IGIs, mangabey whole-group IGIs and mangabey subgroup IGIs (with group identity and observation period as the crossed random effects). I transformed site feeding intensity (square root), food abundance (square root), distribution (log) and patch size (log) to achieve normal distributions of these variables.

There was no multicollinearity among the independent variables in the multilevel models, evidenced by low variance inflation factors (range 1.00–4.12) and condition indexes (range 3.66–3.70; Tabachnick & Fidell 2007). All tests were two tailed, with $\alpha = 0.05$, and performed in STATA v.12 (StataCorp LP, College Station, TX).

Ethical Note

Permissions to conduct this study were granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology and the Uganda Office of the President. Data collection protocols were approved by the Institutional Animal Care and Use Committees of Columbia University (AC-AAAA8112) and the University of New Mexico (11-100661-MCC), and I conducted all research activities in compliance with Ugandan national laws and ASAB/ABS guidelines for the use of animals in research.

RESULTS

Mangabeys

Prediction 1: the basal area of food stems is higher in core areas than in peripheral areas

The mean basal area of food stems in core and peripheral areas was not significantly different in the six mangabey ranges (Table 2, Fig. 1a). Similarly, the multilevel model indicates that core and peripheral areas did not differ in the basal area of food-bearing stems per quadrat, per observation period (Table 3). Core areas contained more food per quadrat than peripheral areas in only 7% of group-periods (and only for groups M2, M3 and M4), and the reverse was true in 2% of group-periods (i.e. peripheral quadrats contained more food, and only for groups M4 and M6).

Prediction 2: males and females are aggressive more often in core areas than in peripheral areas

Overall, males were aggressive in 84% (27/32) of whole-group and 82% (23/28) of subgroup IGIs; females were aggressive in 25% (8/32) of whole-group and 26% (6/28) of subgroup IGIs. Females never exhibited aggression in the absence of male aggression. Most IGIs occurred in the periphery of the home range (69% of whole-group and 64% of subgroup IGIs), which was not significantly different from the amount of time groups spent in that part of the home range (59% of group scans; one-sample proportion test: whole-group IGIs: $Z = 1.121$, $N = 32$ IGIs, $P = 0.262$; subgroup IGIs: $Z = 0.569$, $N = 28$ IGIs, $P = 0.569$).

The frequency of male and female mangabey aggression was unaffected by home range location: aggression was equally

Table 2
The size of the core and peripheral home range areas, the area sampled in botanical plots within each home range area, and *t* tests to determine whether the basal area (BA) of food stems differed between core and peripheral areas

Species	Group	Core area		Peripheral area		*t*	*df*	*P*
		Size (m^2)	No. plots (%)	Size (m^2)	No. plots (%)			
Mangabey	M1	334 608	33 (25)	1 592 423	107 (17)	0.833	138	0.406
	M2	343 988	18 (13)	1 353 972	52 (10)	−0.131	68	0.896
	M3	485 916	25 (13)	1 137 401	63 (14)	−0.990	86	0.325
	M4	369 511	48 (32)	1 658 001	84 (13)	−0.399	130	0.691
	M5	162 729	26 (40)	1 363 771	52 (10)	−0.984	76	0.328
	M6	184 716	9 (12)	1 072 329	42 (10)	0.324	49	0.747
Redtail	R1	75 504	16 (53)	295 933	37 (31)	−0.035	51	0.972
	R2	94 398	18 (48)	244 492	35 (36)	***−3.395***	***51***	***0.001****
	R3	135 677	22 (41)	284 898	24 (21)	0.144	44	0.886
	R4	48 641	7 (36)	258 246	21 (20)	−0.158	26	0.876
	R5	49 016	7 (36)	296 654	34 (29)	***2.081***	***39***	***0.044***
	R6	62 059	9 (36)	447 004	36 (20)	***−3.130***	***43***	***0.003****

Significant differences are indicated in bold italics; those that are opposite the predicted direction (mangabeys: $\text{core}_{BA} > \text{periphery}_{BA}$; redtails: $\text{core}_{BA} < \text{periphery}_{BA}$) are differentiated with an asterisk.

frequent during IGIs in the core versus the periphery, and resource availability in core versus peripheral areas had no effect on aggression (logistic regression: males: $\chi^2_2 = 2.19$, $N = 60$ IGIs, $P = 0.534$; females: $\chi^2_2 = 1.56$, $P = 0.669$).

Prediction 3: males and females are more aggressive in high-intensity feeding sites than in low-intensity feeding sites, and when overall food abundance is low, feeding sites are patchily distributed and feeding patches are large

Neither males nor females were more aggressive in high-intensity feeding sites than in low-intensity feeding sites, in either whole-group or subgroup IGIs (Table 4). However, males were significantly more likely to be aggressive during whole-group IGIs when the overall abundance of food was low and feeding sites were patchily distributed (logistic regression with food abundance-distribution as the sole predictor: Wald $\chi^2_4 = 6.10$, $N = 32$ IGIs, $P = 0.014$; Fig. 2a, b). Aggression by female mangabeys did not correspond with any of the food-related variables tested in this study. Site feeding intensity was not correlated with food abundance-distribution (indicating that one variable could not be treated as a reasonable proxy for the other), but did correlate with feeding patch size (Table 5).

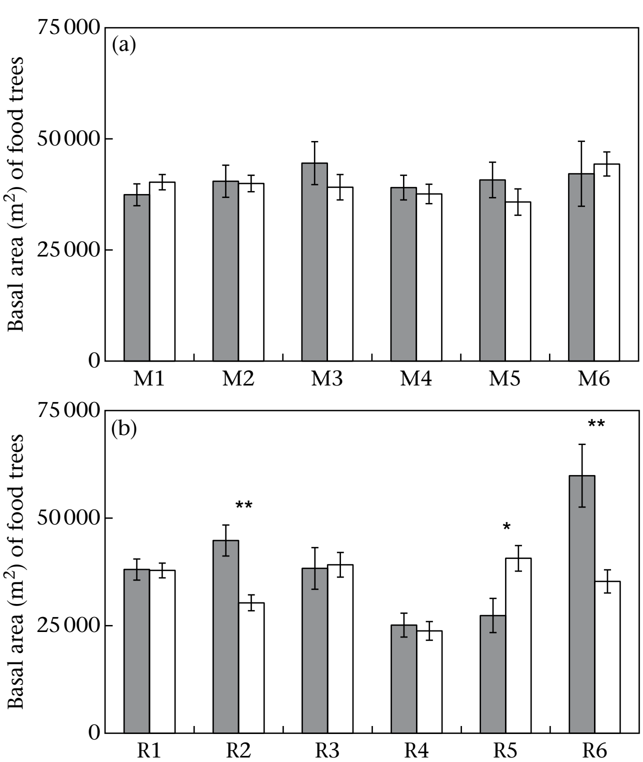


Figure 1. Mean basal area of food trees per quadrat (±SE) in core and peripheral areas for (a) mangabey and (b) redtail groups. Significant differences between core areas (grey bars) and peripheral areas (white bars) are indicated by * ($P < 0.05$) or ** ($P < 0.01$).

Table 3
Linear multilevel models of the differences in the basal area of food-bearing plant stems in core and peripheral areas, per observation period, for mangabeys and redtails

Model parameters	Variable	Coefficient	SE	*P*
Mangabeys (Wald χ^2_{10}=380.76, N=10 271, P<0.001)				
	Core vs periph.	0.054	0.045	0.231
	Group			
	M1 vs M2	0.578	0.061	0.000
	M1 vs M3	0.488	0.054	0.000
	M1 vs M4	−0.310	0.066	0.000
	M1 vs M5	−0.122	0.062	0.047
	M1 vs M6	1.360	0.090	0.000
	Intercept	5.932	0.269	0.000
Redtails (Wald χ^2_{15}=229.35, N=3006, P<0.001)				
	Core vs periph.	−0.070	0.201	0.727
	Group			
	R1 vs R2	−0.490	0.099	0.000
	R1 vs R3	−1.060	0.108	0.000
	R1 vs R4	−0.610	0.179	0.001
	R1 vs R5	−1.140	0.516	0.027
	R1 vs R6	−1.637	0.516	0.002
	Interaction (zone × group)			
	R1 vs R2*	0.254	0.258	0.325
	R1 vs R3*	0.036	0.247	0.886
	R1 vs R4*	2.230	0.384	0.000
	R1 vs R5*	0.304	0.407	0.454
	R1 vs R6*	0.687	0.408	0.092
	Intercept	7.060	0.264	0.000

The categorical 'group' variable indicates whether significant differences existed among group home ranges. The interactions between home range zone and group identity were not significant for mangabeys ($\chi^2_5 = 1.92$, $P = 0.861$) and were dropped from the final model. Quadrat and observation period are included as crossed random effects.

* Interactions tested whether differences between group X and Y varied as a function of home range location.

Table 4
Results of parallel logistic regressions and Wilcoxon two-sample tests to determine whether aggression by male and female mangabeys correlated with individual food characteristics

Model	Predictors	Logistic regression			Wilcoxon test	
		Odds	SE	*P*	*Z*	*P*
Males: whole-group IGIs (Wald χ^2_6=4.91, *N*=32, *P*=0.179)						
	Site feeding intensity	1.002	0.036	0.957	−1.324	0.186
	Food abundance-distribution	***1.364***	***0.146***	***0.033***	−***2.861***	***0.004***
	Food patch size	1.132	0.146	0.399	−0.234	0.815
	Intercept	14.692	1.521	0.077		
Males: subgroup IGIs (LR χ^2_4=6.25, *N*=28, *P*=0.100)						
	Site feeding intensity	0.958	0.023	0.069	1.771	0.077
	Food abundance-distribution	0.948	0.152	0.727	0.900	0.368
	Food patch size	0.958	0.092	0.641	0.751	0.453
	Intercept	22.615	1.286	0.015		
Females: whole-group IGIs (Wald χ^2_6=0.52, *N*=32, *P*=0.915)						
	Site feeding intensity	0.998	0.019	0.924	0.000	1.000
	Food abundance-distribution	1.019	0.063	0.757	0.000	1.000
	Food patch size	0.951	0.101	0.632	0.523	0.601
	Intercept	0.500	0.387	0.370		
Females: subgroup IGIs (Wald χ^2_6=3.35, *N*=28, *P*=0.341)						
	Site feeding intensity	0.263	0.215	0.103	1.177	0.239
	Food abundance-distribution	2.002	2.626	0.597	0.532	0.595
	Food patch size	1.538	0.829	0.424	−0.757	0.449
	Intercept	0.000	0.000	0.179		

IGIs: intergroup interactions. The significant predictor is indicated in bold italics. Note that the model of male aggression in subgroup IGIs did not converge when formulated as a multilevel model, so the random effects were eliminated to yield a fixed effects-only model.

Redtails

Prediction 1: the basal area of food stems is higher in peripheral areas than in core areas

The periphery of the home range contained a greater basal area of food stems than the core in just one of the six redtail ranges; in contrast, the core contained more food than the periphery in two ranges (Table 2, Fig. 1b). Examining variance in the basal area of food-bearing stems across observation periods, home range location (core versus periphery) was not significant (Table 3). There were, however, significant differences among groups and a significant interaction between group identity and home range location ($\chi^2_5 = 40.93$, $P < 0.001$): the food-bearing basal area per quadrat was higher in peripheral areas in 13% of group-periods (and only within the R1, R3 and R5 ranges), and the reverse was true in 26% of group-periods (in the R1, R2, R4 and R6 ranges).

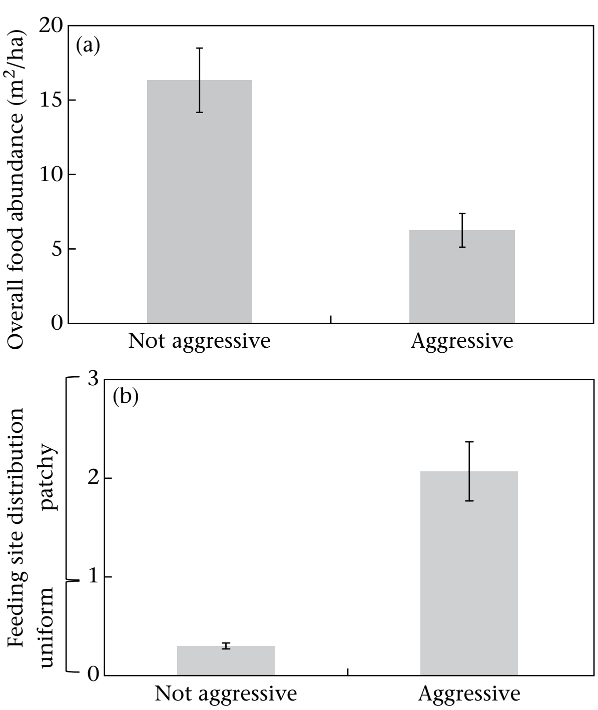


Figure 2. Differences in (a) overall food abundance and (b) feeding site distribution for whole-group intergroup interactions with and without aggression by male grey-cheeked mangabeys.

Table 5
Results of a linear multilevel model to determine whether site feeding intensity correlated with other measures of food availability (abundance-distribution and patch size)

Model parameters	Variable	Coefficient	SE	*P*
Wald χ^2_8=90.25, *N*=192 IGIs, *P*<0.001	Food abundance-distribution	0.035	0.022	0.105
	Feeding patch size	***1.491***	***0.158***	***0.000***
	Intergroup interaction type			
	Mangabey whole group vs mangabey subgroup	−0.579	0.510	0.257
	Mangabey whole group vs redtail whole group	0.563	0.669	0.400
	Intercept	1.756	0.591	0.003

IGIs: intergroup interactions. Interaction type was included as a categorical fixed effect. Group identity and observation period were included as crossed random effects. The significant predictor is indicated in bold italics.

Prediction 2: females (but not males) are aggressive more often during IGIs in peripheral areas than in core areas, largely because IGIs rarely (or never) occur in core areas

Overall, redtail males were aggressive in 33% (43/132) and females in 38% (50/132) of IGIs; in 29% (38/132) of IGIs, both sexes were aggressive. Slightly more than half of all IGIs occurred in the periphery (57%), which did not differ significantly from the amount of time redtail groups spent in that part of their ranges (59% of group scans; one-sample proportion test: $Z = -0.467$, $N = 132$ IGIs, $P = 0.640$).

As was the case for mangabeys, the frequency of male and female aggression was unaffected by home range location: aggression was equally frequent during IGIs in the core versus the periphery, and resource availability in core versus peripheral areas had no effect on aggression (logistic multilevel model: males: Wald $\chi^2_7 = 2.71$, $N = 132$ IGIs, $P = 0.438$; females: Wald $\chi^2_7 = 5.45$, $P = 0.142$).

Prediction 3: females (but not males) are aggressive more often in high-intensity feeding sites than in low-intensity feeding sites, and when overall food abundance is low, feeding sites are patchily distributed and feeding patches are large

Males and females were significantly more likely to be aggressive in high-intensity feeding sites than in low-intensity feeding sites (Table 6). Site feeding intensity was significantly correlated with patch size, but not food abundance-distribution (Table 5). That site feeding intensity predicted male and female redtail aggression, but the other food characteristics did not, indicates that the latter variables were not reasonable proxies for site feeding intensity.

Differences in Food Availability for Mangabeys and Redtails

Because different food variables were important for mangabeys and redtails, I evaluated whether their foods differed in patterns of availability. Compared with redtail IGIs, mangabey whole-group IGIs occurred during periods of relatively low food abundance (linear multilevel regression: Wald $\chi^2_6 = 12.45$, $N = 192$ IGIs, $P = 0.002$). There was no difference among IGI types in the

Table 6
Logistic multilevel models of aggression in male and female redtails

Model parameters	Variable	Odds	SE	*P*
Males (Wald χ^2_6=9.17, *N*=132, *P*=0.027)				
	Site feeding intensity	***1.027***	***0.011***	***0.009***
	Food abundance-distribution	1.047	0.030	0.108
	Food patch size	1.003	0.019	0.896
	Intercept	0.221	0.153	0.029
Females (Wald χ^2_6=10.06, *N*=132, *P*=0.018)				
	Site feeding intensity	***1.025***	***0.010***	***0.010***
	Food abundance-distribution	1.002	0.021	0.916
	Food patch size	1.027	0.020	0.176
	Intercept	0.241	0.108	0.002

Group identity and observation period were included as crossed random effects. Significant predictors are indicated in bold italics.

distribution of values for site feeding intensity (Wald $\chi^2_6 = 1.03$, $P = 0.596$), feeding site distribution (Wald $\chi^2_6 = 2.10$, $P = 0.350$) or feeding patch size (Wald $\chi^2_6 = 1.01$, $P = 0.605$).

The small size of redtail ranges could mean that groups had few alternative food sources (and thus were always forced to aggressively defend the few high-intensity feeding sites available to them), whereas the large mangabey ranges may have usually contained alternative resources, except during the periods of lowest food abundance. However, this did not appear to be the case: there was no difference in the number of mangabey and redtail high-intensity feeding quadrats, regardless of whether overall food abundance was low or high (Table 7).

DISCUSSION

The results of this study fail to support predictions, based on prior studies, that mangabeys exhibit core defence and redtails exhibit periphery defence. Thus, it is not surprising that mangabey core areas did not contain more food resources than peripheral areas, and vice versa for redtails. What is surprising, however, is that neither species can be described with the existing framework of core versus periphery defence: instead, they appear to be following a strategy of ‘patch defence.’ Mangabey males were most aggressive during periods when food resources were most defensible (i.e. feeding patches were few and far between), and redtails were most aggressive during interactions at often-used feeding sites; these patterns were associated with generally equal abundances of food in core and peripheral areas. Moreover, site feeding intensity (the most commonly used indicator of food availability in IGI studies) was not equivalent to food abundance or distribution. Mangabey aggression during subgroup IGIs did not correspond with any food variables, which may indicate an absence of food defence during this type of IGI.

Core, Periphery and Patch Defence

The results presented here contrast with the defence habits of black and white colobus monkeys (Harris 2006) and Tana River crested mangabeys (Kinnaird 1990), for which the core of each

Table 7
Linear multilevel model of the change in the number of high-intensity feeding quadrats across monkey species and changes in overall food abundance (with observation period and group identity as crossed random effects)

Model parameters	Variable	Coefficient	SE	*P*
Wald χ^2_7=73.89,	***Overall food abundance***	***0.474***	***0.071***	***0.000***
N=169 group-periods,	Monkey species	−0.248	0.253	0.327
P<0.001	Interaction (species × abundance)	−0.068	0.107	0.523
	Intercept	0.864	0.147	0.000

The significant predictor is indicated in bold italics.

range contained significantly more food per hectare and was defended more vigorously (and more successfully) than the periphery. The results of this study also contrast with the pattern described for some tamarins and blue monkeys, considered to be ‘territorial’ species, where the periphery likely contains more food per unit area than the core (Garber 1988; Cords 2007). Although most IGIs for these latter species occur in the periphery of the home range (sometimes even occurring in the absence of important, monopolizable food trees; Lawes & Henzi 1995) and their outcomes are determined by mutually recognized boundaries, this does not imply that these groups would be less aggressive or successful in evicting intruders from their core areas. Rather, IGIs occur infrequently in the core because it contains fewer or less desirable resources (which could stem from lower stem densities or higher depletion rates in the core than in the periphery), and possibly because resident groups are able to detect intruding groups before they reach the core. By defending the core or periphery of its home range, a group can increase its likelihood of exclusive access to important resources.

Redtail monkeys are generally described as having territorial intergroup relationships (periphery defence; Struhsaker & Leland 1979), such that deeply intruding groups always retreat from resident groups and explicit boundaries between two ranges can be pinpointed to specific trees (sensu Cords 2007). Territoriality should be impossible at very high densities, however, because neighbouring groups intrude too frequently to allow for the maintenance of exclusive access to important resources, which is the perceived function of territorial boundaries (Dunbar 1988). Interspecific feeding competition could also weaken the feasibility of territoriality if other, sympatric species not only consume the same resources, but also have priority of access to important feeding sites. As the density of Ngogo redtail groups is currently very high (Lwanga et al. 2011) and these groups must also contend with a high degree of feeding overlap with mangabeys, blue monkeys and chimpanzees (Conklin-Brittain et al. 1998), to whom they are subordinate (Houle et al. 2010), classical territoriality may not be feasible for this particular population of redtails.

Quantifying Primate Food Resources

I measured site feeding intensity (as per Fashing 2001; Sicotte & MacIntosh 2004; Korstjens et al. 2005; Harris 2010) to determine whether it was equivalent to measures of food abundance, distribution and patch size (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997), and found that it was not. Had I evaluated only site feeding intensity, I would have concluded that mangabeys do not defend food resources; conversely, had I evaluated only abundance, distribution and patch size, I would have concluded that redtails do not defend food resources. These results demonstrate the importance of considering both sets of variables in analyses of primate intergroup interactions.

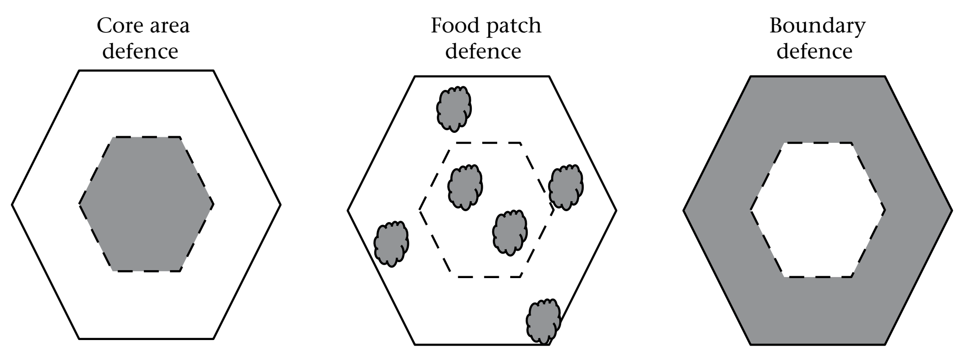
Whereas site feeding intensity and patch size were local variables, specific to the IGI location, food abundance and distribution captured patterns of food availability throughout the home range. The fact that redtail aggression corresponded with site feeding intensity may mean that they are constantly food-limited, not just when the overall abundance of food resources is low (e.g. individuals lost fat reserves around the hips, shoulder blades and tail vertebrae for many months, and newborn infants disappeared at a rapid rate; personal observations). That mangabey male aggression occurred when food abundance was low and feeding sites were patchily distributed suggests the opposite: that they (or their mates) are food-limited during only a few, distinct periods. These contrasting patterns could be tested by tracking C-peptide levels, an indicator of energetic balance (Sherry & Ellison 2007; Deschner et al. 2008; Girard-Buttoz et al. 2011), for both species across different seasons.

In contrast to the primate-centric hypotheses described here, more general models of vertebrate sociality predict differing relationships between food patterning and defence. For instance, Ostfeld (1985, 1990) predicts female territoriality when food is 'sparse, patchy, and slowly renewed'. By contrast, Emlen & Oring (1977) predict monogamous territoriality when resources are 'abundant and stable through time', and male territoriality (resource defence polygyny) when resources are 'unevenly distributed or spatially clumped'. Although Ostfeld was concerned with solitary animals, it is clear that different spatial patterns of availability can lead to food defence. It may be unreasonable to expect that feeding sites are defensible only when they meet a particular set of criteria regarding abundance, distribution and patch size (as predicted by Wrangham 1980; van Schaik 1989; Sterck et al. 1997).

A New Model of Food Defence by Group-living Primates

The pattern to emerge from this and previous studies (Harris 2006, 2010; Kinnaird 1990, 1992) indicates that the type of food defence practised by a group or population (whether defence of a core area, important food patches or the home range periphery) arises from the relative abundance of resources in the core versus periphery (Fig. 3). If core areas contain a greater quantity of important food species per hectare than the periphery, groups should be more aggressive (and more likely to win interactions) in their core areas. Conversely, if peripheral areas contain more food per hectare than core areas, groups should be strongly aggressive in the periphery (in large part because interactions should rarely occur in core areas). Finally, if the quantity of food per hectare in core and peripheral areas is generally equal, groups should defend neither the periphery nor the core and should instead defend important food patches as they become available, regardless of their location in the range.

The few primate studies that have evaluated patterns of intergroup aggression in relation to food availability appear to fall into two main sets: those for which site feeding intensity corresponds with food defence, and those for which food abundance, distribution and/or patch size correspond with food defence (Fig. 3). The most notable difference between these sets of populations is in their group density; dividing group density by mean home range size for each population yields an index of intruder pressure (I_i). Among populations with a high intruder index (>10), site feeding intensity is (or is expected to be) a significant predictor of focal group aggression: e.g. eastern black-and-white colobus (Harris 2005, 2006); redtail monkey (this study); blue monkey (Lawes & Henzi 1995; Cords 1990, 2007; Fashing & Cords 2000); and ringtail lemur (Pride et al. 2006). Among populations with a low intruder index (<10), overall food abundance, feeding site distribution and/or patch size are (or are expected to be) significant predictors: e.g. Tana River crested mangabey (Kinnaird 1990, 1992); white-faced capuchin (Crofoot 2007; Crofoot et al. 2008); grey-cheeked mangabey (this study); green monkey (Harrison 1983); chimpanzee (Emery Thompson et al. 2009; Wrangham 1975); and spider monkey (Wallace 2008). This dichotomy implies that when intruder pressure is particularly high (and groups are presumably food-limited year round), intensely utilized feeding sites are defended regardless of food abundance, distribution or patch size. Conversely, when intruder pressure is low, group defence corresponds more directly with conventional measures of economic defendability (Brown 1964), and resources are defended only during discrete periods of food limitation. Although $I_i = 10$ is a convenient threshold for the populations listed in Fig. 3, in reality, we should expect to find a continuum along which site feeding intensity and food abundance/distribution/patch size vary in their biological significance as predictors of aggression.



	$Core_{BA} > Periphery_{BA}$	$Core_{BA} = Periphery_{BA}$	$Core_{BA} < Periphery_{BA}$
Site feeding intensity (Intruder index > 10)	Eastern black and white colobus (68.2)[1]	Redtail monkey (18.3)[2]	Blue monkey* (21.7)[3] Ringtail lemur* (190.9)[4]
Food abundance & distribution & patch size (Intruder index < 10)	Tana River mangabey (4.1)[5‡] White-faced capuchin* (1.1)[6]	Grey-cheeked mangabey (0.9)[2] Green monkey* (0.1)[7]	Chimpanzee* (<0.01)[8] Spider monkey* (0.2)[9]

Figure 3. The proposed relationships among food availability in core and peripheral areas (measured as the basal area (BA) of food stems), defence patterns (core, patch and periphery defence) and fine-grained food characteristics (site feeding intensity, food abundance, feeding site distribution and food patch size). The hexagons represent home ranges in which the dashed and solid lines enclose the core and peripheral feeding areas. Dark shading indicates areas of high food basal area. In parentheses: the intruder index (group density (groups/km^2) ÷ mean home range size (km^2)) of the study population. Species with asterisks (*) are those for which data are not yet available on the relative quality of core and peripheral feeding areas. [1] Harris (2005, 2006); [2] this study; [3] Cords (1990, 2007), Fashing & Cords (2000), Lawes & Henzi (1995); [4] Pride et al. (2006); [5] Kinnaird (1990, 1992); [6] Crofoot (2007), Crofoot et al. (2008); [7] Harrison (1983); [8] Emery Thompson et al. (2009), Wrangham (1975); [9] Wallace (2008). [‡] The group density for Tana mangabeys is about 1.5 groups per 20 ha (rather than groups/km^2) because there were only two groups that used the Mchelelo forest fragment, and one of these groups spent just 45% of its time inside the fragment.

In addition to testing the framework proposed here with a broader array of species, an important issue is to determine what causes groups to establish core areas in locations of high, low or average food availability. Unlike most other vertebrates, primate groups tend to reside in stable home ranges for many generations (Jolly & Pride 1999), but it is nonetheless possible to study how home ranges are initially placed in the environment by tracking the establishment of new groups resulting from fission events (Janmaat et al. 2009). In all likelihood, it is a combination of group density, habitat structure and interspecific competition that give rise to these variable patterns of food availability in core versus peripheral areas.

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