RESEARCH ARTICLE

Living in Forest Fragments Reduces Group Cohesion in Diademed Sifakas (*Propithecus diadema*) in Eastern Madagascar by Reducing Food Patch Size

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Forest fragmentation is thought to threaten primate populations, yet the mechanisms by which this occurs remain largely unknown. However, fragmentation is known to cause dietary shifts in several primate species, and links between food resource distribution and within-group spatial dynamics are well documented. Thus, fragmentation has the potential to indirectly affect spatial dynamics, and these changes may present additional stresses to fragmented populations. I present the results from a 12-month study of *Propithecus diadema* at Tsinjoarivo, eastern Madagascar, including two groups in fragments and two in continuous forest. Instantaneous data on activity and spatial position were collected during all-day focal animal follows. Fragment groups had much lower cohesion, being more likely to have no neighbor within 5 and 10 m. For continuous forest groups, cohesion was highest in the rainy season (when food patches are large) and lowest in winter (when the animals rely on small-crowned mistletoes), and the chance of having no neighbor within 5 m was positively correlated with mistletoe consumption. Thus the decreased cohesion in fragment groups is inferred to result from their increased reliance on mistletoes and other small resources, which causes them to spread out among multiple patches. This scenario is consistent with the reduced body mass of subordinate individuals (males and immatures) in fragments, and suggests the occurrence of steeper within-group fitness gradients. Further research is necessary to determine whether these patterns apply to other primates; however, since fragmentation tends to cause the loss of the largest trees, many primates

INTRODUCTION

Habitat destruction is one of the most pervasive causes of biodiversity loss in the tropics [Laurance, 1999]. Although habitat loss and fragmentation can be assessed quite easily using satellite images [Jorge & Garcia, 1997], little is known about exactly how fragmentation leads to species extinctions [Laurance et al., 2002]. Habitat fragmentation affects animal populations on several levels and time scales: a direct anthropogenic impact (such as hunting) threatens most immediately, altered habitat characteristics can affect the ecological fit between animals and their environment, and spatial discontinuity of habitat can affect population genetics and demography over the long term [Turner, 1996].

Although many authors have shown that primate species vary in their susceptibility to fragmentation [Ganzhorn et al., 2003; Gilbert & Setz, 2001; Onderdonk & Chapman, 2000], little is known about the ecological bases of this variation. Some authors have suggested that behavioral plasticity [Dehgan, 2003] may be more important than static measures of species' characteristics (e.g., body size, diet, and life history); in other words, species' characteristics in intact forest may not accurately predict their behavior, and hence their viability, in fragments. It is currently impossible to adequately address this question, since almost no long-term ecological studies of primates in forest fragments have been conducted [Estrada et al., 1999; Menon & Poirier, 1996].

To date, no study has examined the effects of fragmentation on within-group spatial dynamics in primates. However, several studies have documented fragmentation-related changes in diet, including shifts in the plant parts [Singh et al., 2001; Tutin, 1999; Umapathy & Kumar, 2000a; Irwin, 2006] and plant species [Onderdonk & Chapman, 2000] consumed. Thus, the potential exists for changes in ranging and spatial dispersion, to the extent that these depend on the distribution of food resources.

Several studies have illustrated the importance of resource patch size, density, and distribution in determining group size, subgroup size, and food patch use [Chapman, 1990a; Overdorff, 1996], as well as competitive regimes and social relationships [Sterck et al., 1997]. The positive relationship between patch size and feeding subgroup size is well supported empirically [Leighton & Leighton, 1982; Overdorff, 1996; Stevenson, 1998], but the relationship between patch size and group cohesion is complex. When patches are large enough to accommodate many foraging animals, decreasing patch size should increase cohesion, as groups are forced into smaller spaces to feed. However, when patches are smaller, the opposite effect may be observed: when small patches limit subgroup size (due to spatial/structural limitations, agonistic exclusion, or deference by subordinates) groups will fragment and cohesion may decrease. In this case, some species form "fission-fusion" societies in which subgroups travel independently (*Ateles* [Chapman, 1990b] and *Pan* [Lehmann & Boesch, 2004]), while other species travel together but increase group spread and use several patches simultaneously (*Cebus capucinus* [Phillips, 1995]). In extreme cases in which single animals use patches, decreased group cohesion should be accompanied by increased nearest-neighbor distances. The nature and direction of such shifts will depend on the

specific effects fragmentation has on resource distributions, as well as a species' characteristics, such as its group size and social system.

The spatial compromises that occur when group spread is considerably larger than food patch size can have several fitness consequences. First, they may accentuate dietary differences between dominants and subordinates, since subordinates may feed on nearby lower-quality patches rather than more distant high-quality patches (aggression will not necessarily be apparent [Vogel, 2005]). This may cause a steeper fitness gradient among individuals, and may alter within-group competitive regimes, demography, and/or distribution of reproductive success. Additionally, reduced cohesion may dilute the benefits of group living, particularly in terms of predator detection and protection from infanticide [Janson, 1992; van Schaik & Janson, 2000]. Finally, interactions with several other fragmentation-related effects may occur. For example, demography may change due to constrained dispersal and/or altered mortality and reproductive rates, leading to an altered ''neighborhood'' of interaction partners [Umapathy & Kumar, 2000b]. An individual's health (which can be affected by altered diet and disease/parasitism regimes [Chapman et al., 2005; Gillespie & Chapman, 2006]) may also affect that individual's willingness to compete for resources, thereby affecting competitive regimes within and between groups.

This paper examines the effects of forest fragmentation on the within-group spatial ecology of a critically endangered primate, the diademed sifaka (*Propithecus diadema*), at Tsinjoarivo, Madagascar. This population spans an ecological gradient from intact primary forest to isolated, small fragments degraded by a combination of natural and anthropogenic impacts. Specifically, I examined 1) how forest fragmentation affects group cohesion, as measured by nearest-neighbor distances; 2) activities in which changes in group cohesion were most pronounced; 3) differences among age/sex classes in neighbor identity and distance; 4) seasonal variation in group cohesion; and 5) whether changes in nearest-neighbor distances can be related to food resource characteristics.

MATERIALS AND METHODS

Study Site

Tsinjoarivo forest is located southeast of Ambatolampy on the escarpment that divides Madagascar's central plateau and eastern lowlands, and about 80 km SSE of Antananarivo. The region contains unprotected central domain mid-altitude rainforest [Koechlin et al., 1974] in the corridor between Ranomafana (150 km SSW) and Mantadia National Parks (100 km NE). The corridor's western half has been fragmented and degraded by settlers from the central plateau, while the eastern half has been only minimally disturbed [Irwin, 2006].

I established two research camps at Tsinjoarivo, separated by 12 km. Mahatsinjo (19°40.94′S, 47°45.46′ E, 1590 m), in the corridor's western half, contains hill- and ridge-top forest fragments. Lower lands surrounding the fragments contain settlements, cultivated land, grass, and secondary forest. Vatateza (19°43.25′S, 47°51.41′ E, 1396 m) is within continuous forest in the corridor's eastern half, and human settlements are nearby in the Onive river valley to the south. The fragments at Mahatsinjo show reduced physical structure (tree density, crown volume, and basal area per hectare) and tree diversity relative to the continuous forest at Vatateza [Irwin, 2006]. These changes likely resulted from a combination of anthropogenic and natural impacts after fragmentation. Anthropogenic extraction has been extensive (mainly for house

and oxcart construction, and rum distillation [Irwin, 2006]), but the relative contribution of natural forces [Laurance et al., 2002] remains unknown.

There is a distinct rainy season between December and March, and a dry season between April and November at both sites. The annual rainfall at Vatateza totals 2,610 mm, of which an average of 1,604 mm (61.5%) falls during the rainy season. The annual rainfall at Mahatsinjo is lower (1,724 mm), with 1,066 mm (61.9%) on average falling during the rainy season. Temperatures are highest in December–January and lowest in June–August [Irwin, 2006].

Study Population

Tsinjoarivo sifakas are currently considered members of the critically endangered species *Propithecus diadema* [Mayor et al., 2004], although body mass and morphometric and pelage differences suggest that they may be a distinct subspecies [Irwin, 2006] (Glander & Irwin, unpublished data). They live in small social groups of two to six individuals (excluding infants <1 year old). In group size and composition they are similar to *P. edwardsi* at Ranomafana [Pochron & Wright, 2003; Pochron et al., 2004] and *P. diadema* at Mantadia [Powzyk, 1997].

Four groups were examined for this study: two in continuous forest at Vatateza (CONT1 and CONT2) and two in fragments at Mahatsinjo (FRAG1 and FRAG2). Group size was similar between sites during the study (CONT1: n = 6–7, CONT2: n = 5–6, FRAG1: n = 4–5, and FRAG2: n = 5), and all groups had two breeding adults (one male and one female), except CONT2 (one male and two females). As with other sifakas, females are dominant over males (dominance hierarchies were constructed using aggressive interactions [Irwin, 2006]). CONT groups had larger home ranges (70–80 ha) than FRAG groups (20–37 ha) [Irwin 2006]. The diet of these groups is well known [Irwin, 2006]. The most important resource in terms of feeding time is the hemiparasitic mistletoe *Bakerella clavata* (Loranthaceae), which roots directly in host trees and has a small crown (typically <2 m in diameter). Continuous forest groups use this species as a fallback resource during the time of fruit scarcity (July–October, when they consume leaves and flowers), while fragment groups use it heavily all year (consuming leaves, flowers, and fruit).

Animals in all groups were captured using the Pneu-dart™ system and disposable darts loaded with Telazol® (following Glander et al. [1992]). One or two animals per group were given radio collars (Telonics, Mesa, AZ; weight ≤35 g), and all other animals captured were given colored olefin collars and metal pendants. All animals could be reliably identified because no group had more than one uncollared individual per size class (adult, subadult/juvenile, or infant). Groups were habituated during December 2002 and could be observed reliably at close distances during the study.

Behavioral Data Collection

Behavioral data were collected between January and December 2003. Groups CONT1 and CONT2 were followed during the first 2 weeks of each month, while FRAG1 and FRAG2 were followed during the last 2 weeks (mean = 13.6 follows/group/month). The single exception was June, when CONT groups were followed from 14 to 20 June, and FRAG groups were followed from 24 June to 2 July (mean = 6.5 follows/group). Observations were made during day-long focal animal follows conducted by myself and a local assistant, or one to two trained research assistants with one local assistant. Focal animals included animals that were >1.5 years old in January 2003, and were selected on a

rotating basis to equalize sample size among individuals. I worked with all assistants, and standardized data collection and distance estimation with interobserver reliability checks.

Instantaneous activity data were collected at 5-min intervals. At each interval, observers recorded the focal animal's activity and nearest-neighbor identity and distance. Activity was recorded as "rest" (alert, inactive, self-groom, or scratch), "social" (groom, vocalize, or aggression), "travel" (within tree, tree to tree, or pause during travel), or "feed" (food species and item were recorded). Nearest-neighbor distances were recorded categorically (in contact: "0 m"; 0–10 m: visually estimated to the closest of the following distance classes: 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10 m). When the nearest neighbor was >10 m away, no neighbor was recorded (visibility conditions made detection beyond this distance unreliable). Animals were considered solitary when the nearest neighbor was >5 m away.

Habitat Sampling

Forty 0.1-ha sample plots were inventoried. Ten of these were within each group's home range, which constitutes 3–5% of the home ranges for FRAG groups and 1.25% for CONT groups. For stems ≥5 cm diameter at breast height (DBH), I recorded species, DBH, height, and the incidence of hemiparasites and hemiepiphytes (including *Bakerella clavata*), and estimated crown height, and two crown diameters (maximum and perpendicular) [Irwin, 2006] (Irwin, unpublished results). Crown volumes were estimated using the formula for an ellipsoid.

Data Analysis

Analyses were based on 651 individual-days encompassing 6,464 hr of contact time (average 9.9 hr/day), and 80,212 activity records (relatively evenly split among groups, individuals, and months). Of these records, 77,563 (97%) contained data for nearest-neighbor distance (the remaining records were discarded). Of the 56,768 records for which a neighbor was recorded, its identity was known in 53,826 (95%).

To investigate differences among groups, I analyzed monthly averages for individual animals using a two-factor repeated-measures analysis of variance (ANOVA), with months as blocks [von Ende, 2001]. This repeated-measures approach was necessary because diet and behavior varied among months, and many data sets showed significant departures from sphericity. To test relationships between diet and nearest-neighbor characteristics (on a monthly basis), I used Spearman rank-order correlations [Siegel & Castellan, 1988], since some variables were not normally distributed (Kolmogorov-Smirnov test for normality).

Plant distributions were compared by means of species' density (ind./ha), average DBH and crown volume, and Lloyd's indices of mean crowding and patchiness [Pielou, 1969]. Lloyd's index of mean crowding represents an individual's average number of conspecifics within a sample plot. Thus, if plot size is similar to group spread (as is the case here), this index should approximate the number of nearby patches of a given species. Since this index scales positively with density, Lloyd's index of patchiness (= Lloyd's index of mean crowding/mean density) was used to provide a scale of patchiness that is independent of resource density (higher values represent more "clumped" distributions).

I investigated neighbor tolerance by examining the identity of adult females' nearest neighbors. Because they are dominant, adult females control access to resources and therefore have the most direct influence on group spacing. Deviations from random neighbor choice were assessed with the use of a G-test for goodness of fit [Sokal & Rohlf, 1995].

RESULTS

Nearest-Neighbor Distances

When all behavioral contexts (i.e., activity classes) were considered, FRAG groups had greater nearest-neighbor distances than CONT groups (Fig. 1). FRAG animals were less likely to have a neighbor within 5 m (FRAG: 41–47%, CONT: 64–68%) and 10 m (FRAG: 60–66%, CONT: 83–86%). When only "feed" records were considered, the difference was more pronounced (Fig. 1b). While animals in CONT groups often fed with a neighbor between 0.5 and 5 m (65–67%), FRAG groups were less likely to have a neighbor that close (34–39%). Finally, the frequency of having no neighbor within 10 m was higher in FRAG groups (39–43%) than in CONT groups (15–17%). The frequency of having no neighbor within 5 m differed significantly between sites, and this difference was significant in all contexts except "social" (Table I).
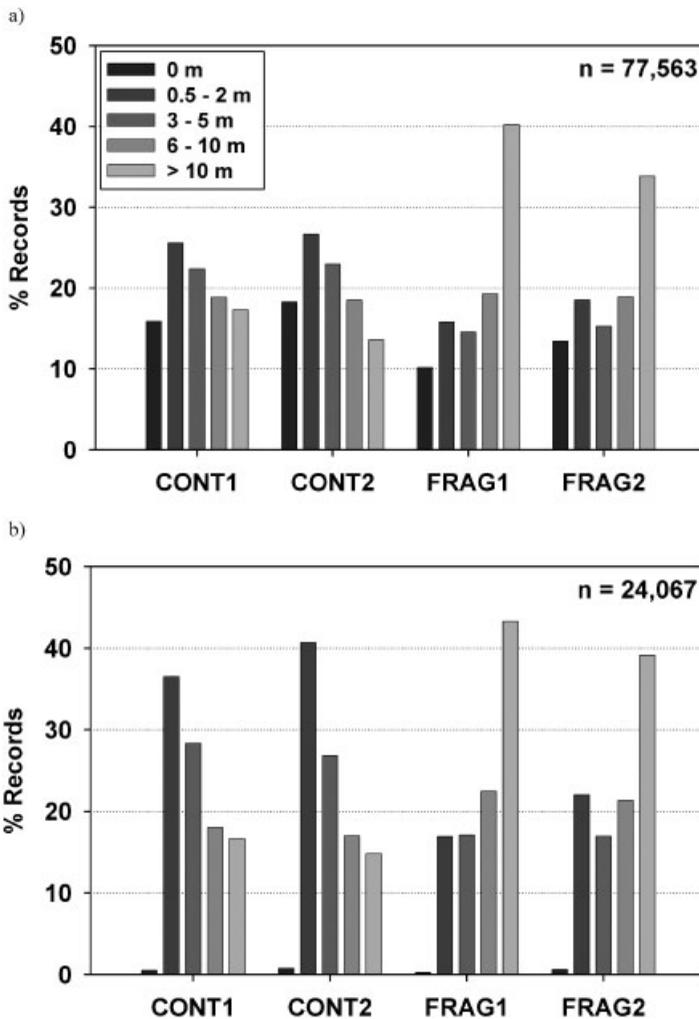

Fig. 1. Nearest-neighbor distances in all contexts (**a**) and feeding contexts (**b**).

TABLE I. Frequency of Being Solitary (% Records Having No Nearest Neighbor Within 5 m) in Different Behavioral Contexts (Mean ± SD of Individual Animals: 10 CONT, 8 FRAG)

	CONT	FRAG	Magnitude of increase between sites	Significance[a]
All activities	34.1 ± 6.2	55.9 ± 8.3	64%	F = 37.02 $P < 0.001$
Feed	33.6 ± 7.0	63.5 ± 7.7	89%	F = 59.68 $P < 0.001$
Rest	36.4 ± 7.1	53.5 ± 9.4	47%	F = 17.82 $P = 0.001$
Social	5.9 ± 6.4	10.0 ± 9.9	68%	F = 0.82 ns
Travel	44.6 ± 7.5	71.1 ± 7.9	60%	F = 24.92 $P < 0.001$

CONT, continuous; FRAG, fragments; SD, standard deviation; ns, not significant.
[a]Two-Factor Repeated Measures ANOVA using individual animals and blocking over months (n = 12); CONT: n = 8 animals (two animals dispersed during the study), FRAG: n = 8 animals; all variables arcsine-transformed.

Seasonality of Solitariness

If group cohesion is driven by food-resource characteristics, it follows that cohesion should change seasonally, following seasonal changes in diet. Figure 2a shows the monthly frequencies of being solitary (i.e., no neighbor within 5 m). FRAG groups consistently had a higher frequency (41–68%) than CONT groups (21–45%). The most notable seasonal trend is a decreased solitariness during the dry season (June–August, both habitats). In feeding contexts (Fig. 2b), the difference is greater and seasonal variation is more evident. The frequency of solitary feeding was consistently higher in FRAG groups (52–76%) relative to CONT groups (17–43%). CONT groups had a low solitary feeding rate during January–March, and a higher rate during the rest of the year. In FRAG groups there was little seasonal variation apart from a tendency to be more solitary in January.

Importance of Mistletoes in Determining Cohesion

There was a positive correlation between monthly average mistletoe consumption and solitary feeding for CONT groups (CONT1: $r_s = 0.706$, $P = 0.01$; CONT2: $r_s = 0.629$, $P = 0.03$), but not for FRAG groups (FRAG1: $r_s = -0.105$, $P = 0.75$; FRAG2: $r_s = 0.154$, $P = 0.63$). Mistletoes are distinct from other favored resources in that they have much higher densities and smaller crowns (Table II), though this difference was more pronounced for CONT groups. The contrast in patch size is probably even greater than indicated by average crown volumes, because fruiting individuals of tree species (especially *Ocotea* sp. 1) tended to be larger than average. In addition, the mistletoes' high density led to high indices of mean crowding relative to other resources, despite low or moderate patchiness.
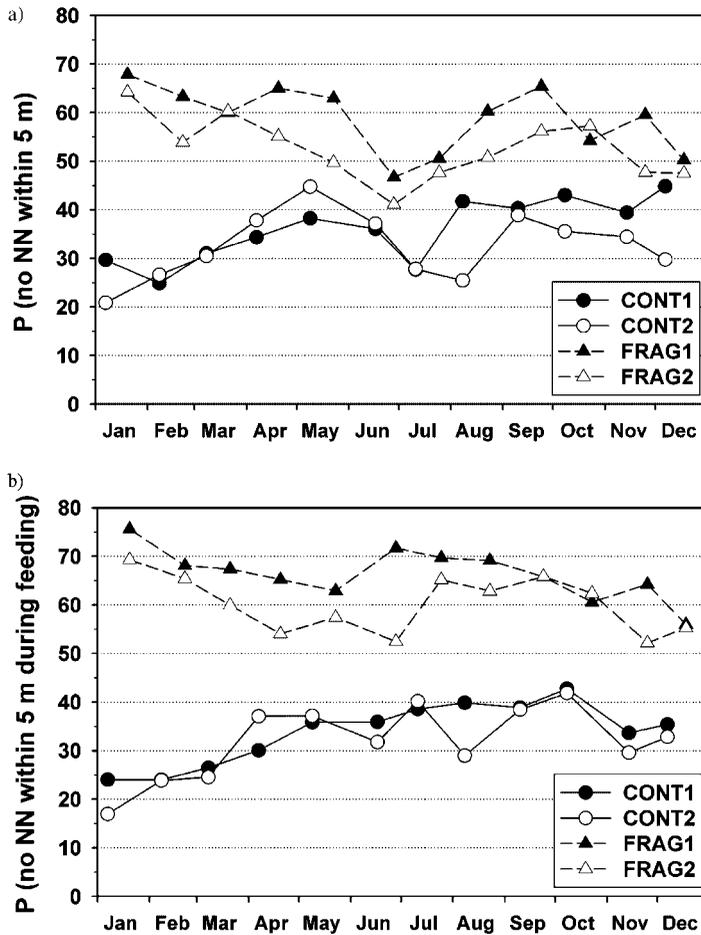
Fig. 2. Monthly variation in the frequency of having no nearest neighbor within 5 m during all contexts (**a**) and feeding (**b**).

Nearest-Neighbor Identity: Relationships

The neighbors of the four dominant adult females were not a random sample of group members (Fig. 3). All observed distributions deviated significantly from expected frequencies, based on group mates being randomly selected as nearest neighbors (G-test, $P < 0.001$). The patterns for all contexts and feeding records were similar. Adult males were the nearest neighbor less often than expected, and only the youngest immatures (on the far right of each plot) maintained proximity more than expected. These animals were either 0.5 (CONT1: PR, CONT2: PS, FRAG2: PG), or 1.5 years old (FRAG1: PB) in January 2003.

The subordinate female (RAD) in CONT2 displayed a very different pattern. All immatures and the adult male were RAD's neighbor at near-expected or higher-than-expected rates, but the dominant female (TG) was RAD's neighbor less often than expected (this relationship was reciprocal: RAD was TG's neighbor less often than expected). The lack of affiliation between these two females may not be a general rule for sifaka groups, and the degree of tolerance may depend on relatedness.

TABLE II. Patch Characteristics of the Top Five Food Species of CONT and FRAG Groups

	% Feeding time[a]	Density (ha^{-1})	DBH (cm)	Crown volume (m^3)	Index of mean crowding/patchiness[e]
CONT					
Bakerella clavata	28.65	98.5	–	$\leq \sim 5^c$	16.64/1.69
Ocotea sp. 1	9.53	19.5	19.3 (5.3–54)	43.3 (0.5–205.3)	2.67/1.37
Garcinia sp.	5.44	74.5	20.8 (5.8–66)	35.1 (0.5–263.9)	16.21/2.18
Pittosporum verticillatum	4.58	9.5	10.1 (5.0–19)	13.2 (1.0–37.7)	1.37/1.44
Salacia madagascariensis	4.36	5.0	6.5 (5–9)	–^{d}	0.60/1.20
FRAG					
Bakerella clavata	34.98	151.5	–	$\leq \sim 5^c$	18.89/1.25
Melicope sp.	14.44	23	12.4 (5.1–40.7)	27.8 (0.5–197.9)	7.48/3.25
Schefflera sp.	5.51	17	12.3 (5.2–25.4)	26.1 (0.5–219.9)	3.53/2.08
Macaranga ankafinensis	4.56	52	7.5 (5–21.4)	15.1 (0.5–109.9)	9.94/1.91
Embelia concinna	3.83	–^{b}	–	–	–

CONT, continuous; FRAG, fragments.
*Density, DBH, crown volume and coefficient of dispersion (CD) are derived from 40 0.1-ha botanical inventory plots (20 plots in CONT habitat, 20 in FRAG habitat). For DBH and crown volume, mean and range are given.
[a]Average values of two groups per habitat.
[b]*Embelia concinna* is a liana; due to small DBH (<5 cm) it was not reliably assessed in the plots.
[c]Not directly quantified but mistletoes exceeding 2 m in diameter were rare.
[d]*Salacia madagascariensis* is a semi-independent climber; thus crown volume is irregular and hard to estimate.
[e]Lloyd's Indices of mean crowding and patchiness [Pielou, 1969].

Finally, adult males tended to be more solitary than females, and foraged alone more frequently than females at the same site (Table III). This is consistent with dominant females' tolerance of immatures, but not males, at feeding sites.

DISCUSSION

FRAG groups had reduced group cohesion relative to CONT groups, and this difference was most pronounced during feeding contexts, which suggests that food resource distribution was driving the change. The increases during ''rest'' and ''travel'' were expected, since these categories capture feeding-related search activities (because of the sifakas' intermittent locomotion, many ''rest-alert'' records captured pauses in locomotion). The counterintuitive increase in ''social'' may be due to the inclusion of vocalizations, since FRAG animals often gave ''lost calls'' when separated from their group.

All groups showed decreased solitariness during the dry season, most likely because activity periods were reduced during this time, and more records involved animals in sleep trees. Solitariness during feeding also varied seasonally, particularly for CONT groups. Both the overall difference between habitats and the observed seasonality are consistent with observed botanical and dietary differences [Irwin, 2006]. CONT groups had a low solitary feeding rate during January–March (rainy season), when they relied on the fruits of large trees, such as *Ocotea* (Lauraceae) and *Erythroxylum* (Erythroxylaceae) [Irwin, 2006]. At this time, dominants tolerated the proximity of group members, probably because larger food patches made defense impractical and/or uneconomical. The solitary feeding rate was higher during the rest of the year, especially during the early and
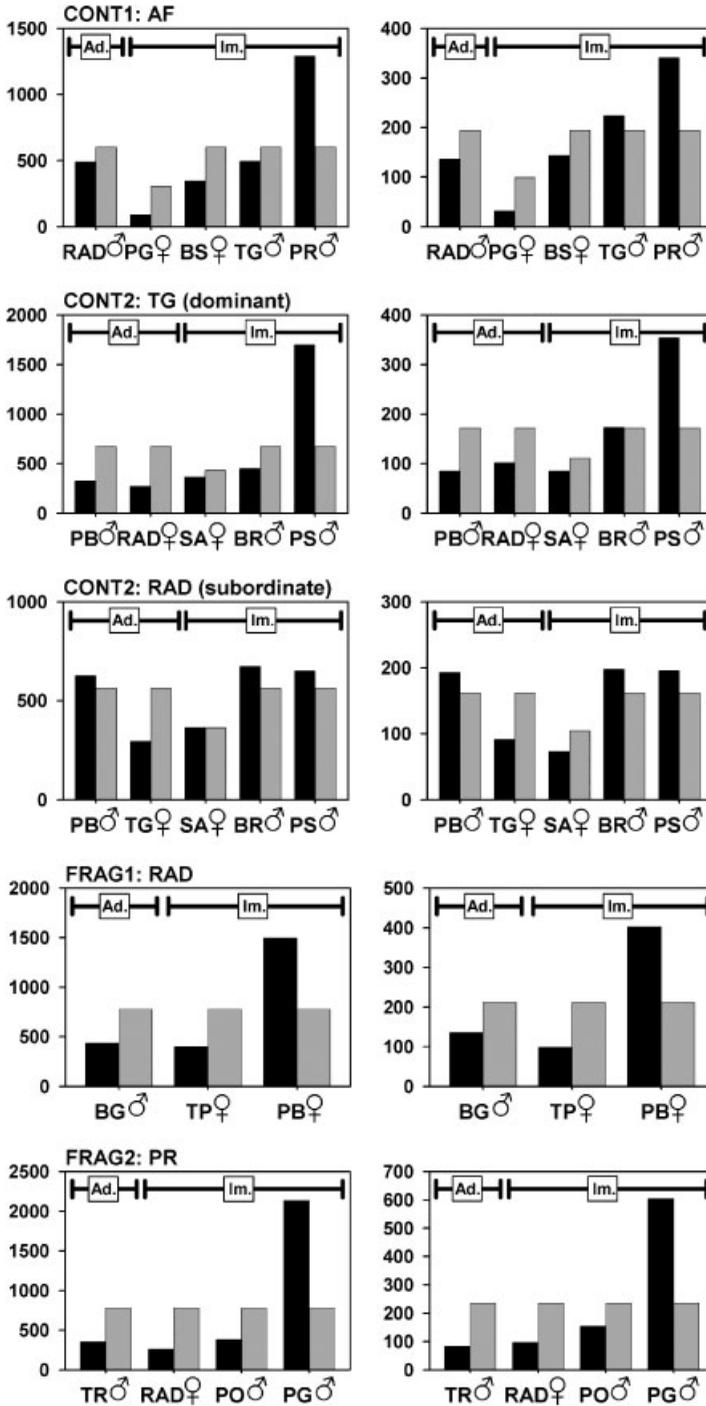
Fig. 3. Identity of nearest neighbors for all adult females during all contexts (left) and feeding contexts (right). Black bar: Observed frequencies (♯ records). Gray bar: Expected frequencies if all group mates were equally likely to be the neighbor (adjusted for animals that left the group during the study). Horizontal lines indicate adults and immature animals (ordered from oldest to youngest).

TABLE III. Sex Differences in the Frequency of Being Solitary (% Records with No Nearest Neighbor Within 5 m) While Feeding: Individual Animals and Summaries (Mean ± SD)

	Female	Male
CONT	CONT1 AF: 28.7	CONT1 RAD: 37.5
	CONT2 TG: 24.6	CONT2 PB: 46.5
	CONT2 RAD: 31.6	
Mean ± SD	28.3 ± 6.5	42.0 ± 6.4
FRAG	FRAG1 RAD: 68.4	FRAG1 BG: 70.2
	FRAG2 PR: 49.0	FRAG2 TR: 66.2
Mean ± SD	58.7 ± 13.7	68.2 ± 2.8

CONT, continuous forest; FRAG, fragments; SD, standard deviation.

late dry season (when young leaves were the main food) and mid-dry season (when the small-crowned mistletoe *B. clavata* was the main food species). In contrast, FRAG groups showed little seasonal variation, though they were most solitary in January (when the main food was *Macaranga ankafinensis*, a small understory tree).

CONT groups therefore undergo considerable seasonal variation in resource patch characteristics. The fruiting trees utilized in the rainy season were rare but large, with typical diameters on the order of 10 m (crown volume > ~500 m^3). In contrast, the mistletoes utilized in the dry season were common but small, and rarely exceeded 2 m in crown diameter (crown volume = ~4.2 m^3). This contrast is consistent with the CONT groups' increase in solitary foraging with increasing mistletoe consumption. The animals could not share mistletoes but could locate other mistletoes fairly easily. The positive relationship between mistletoe feeding and solitary foraging in CONT groups is therefore likely due to two factors: First, mistletoe consumption was more variable seasonally in CONT groups (they were eaten rarely in the rainy season, but accounted for almost 70% of feeding time in dry-season months [Irwin, 2006]. Second, the contrast between mistletoe and non-mistletoe patch size was greatest in CONT groups (Table II). For FRAG groups, both the absence of this relationship and the overall decreased cohesion is consistent with their diet: 1) mistletoe consumption was high year-round, and 2) other important resources (often understory/edge trees or epiphytes, e.g., *Macaranga ankafinensis*, *Embelia concinna*, and *Maesa lanceolata*) also tended to be small-crowned.

These results have important implications for dominance relationships and fitness. Since FRAG groups often use multiple patches simultaneously, there is greater potential for dietary differences, since dominants should select higher-quality patches and subordinates should feed in lower-quality patches (assuming that the patches differ in quality, and the animals accurately assess the differences). Because CONT groups more often share large patches, especially in the rainy season, they should experience less within-group variation. Consequently, FRAG groups should have a steeper fitness gradient between dominants (adult females) and subordinates (adult males and immatures). Indeed, preliminary data show that males are 2.8% heavier than females in CONT groups, but 8.0% lighter than females in FRAG groups, and same-aged immatures tend to be lighter in FRAG groups [Irwin, 2006].

Patterns of proximity show that dominant females allowed the youngest offspring to remain close, but eschewed adult males and older immatures. These

patterns held during feeding contexts and all contexts. Although one might expect exaggerated preferences during feeding, all-contexts frequencies were likely similar because of the inclusion of resting and travel records associated with feeding, and sleeping records (animals were selective about neighbors at sleep trees). Thus, protection from resource stress afforded by dominance is extended from females to offspring, but only until they reach 1–2 years of age. During the remaining years before dispersal (at ≥4 years [Irwin, 2006; Pochron et al., 2004]), immatures are submissive to adults and may be the group most at risk of dietary stress. Indeed, preliminary data show similar infant survival rates to 0.5 years in CONT and FRAG groups, but elevated mortality rates for older immatures in FRAG groups [Irwin, 2006].

One might expect higher aggression rates in FRAG groups because of the smaller typical patch size, but FRAG groups had lower rates (FRAG1: 0.079 acts/hr, FRAG2: 0.048 acts/hr) than CONT groups (CONT1: 0.130 acts/hr, CONT2: 0.231 acts/hr) [Irwin, 2006]. This is consistent with *B. clavata*'s high density, which mediates the potential costs of reduced patch size. Rather than compete for occupied *B. clavata* patches, subordinates generally forage in nearby patches, resulting in lower aggression rates.

In summary, this study shows that sifaka group cohesion is reduced in forest fragments, and this reduction is due to a dietary shift involving increased consumption of mistletoes and other small-crowned resources. Rather than competing more for these smaller food patches, the animals spread out to feed simultaneously on multiple patches, an alternative made possible by the high density of the most-consumed resource, *B. clavata*. Changes in body mass suggest that this altered environment has fitness consequences.

However, further research will be necessary to more precisely describe this species' spatial ecology during foraging, and to elucidate the social processes that underlie the spatial patterns. In addition, more research into the fitness consequences of different aspects of fragmentation (e.g., altered diet, ranging, social behaviors, predation pressure, and dispersal) is needed to gauge the importance of spatial changes. If viability is reduced in fragments, as suggested by body mass and demographic data, understanding the direct and indirect mechanisms by which threats act is crucial for conservation efforts.

Further research will also be necessary to determine whether similar shifts (to smaller resource patches) occur in other primate species. Fragmentation and associated disturbances typically kill the largest trees [Laurance et al., 2000], and anthropogenic extraction may exacerbate this problem because humans often target large trees for timber, fuel for brewing stills, and charcoal [Medley, 1993]. Losing the largest food patches may therefore be a general syndrome faced by many primates in fragments. This may affect both frugivorous species, which often rely on mature canopy trees, and folivorous species that show moderate or high selectivity for certain tree species.

Nevertheless, this study illustrates that primate populations are capable of making flexible responses in disturbed and fragmented habitats. Researchers who wish to model primate extinctions in forest fragments should consider such behavioral and ecological shifts. Models based on ''baseline'' values (i.e., population densities, demographic patterns, diet, and social behavior) derived from intact, undisturbed forests will be insufficient. We need to better understand the ecological bases that underlie species' responses if we are serious about avoiding primate extinctions in the increasingly fragmented tropical forests.

ACKNOWLEDGMENTS

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