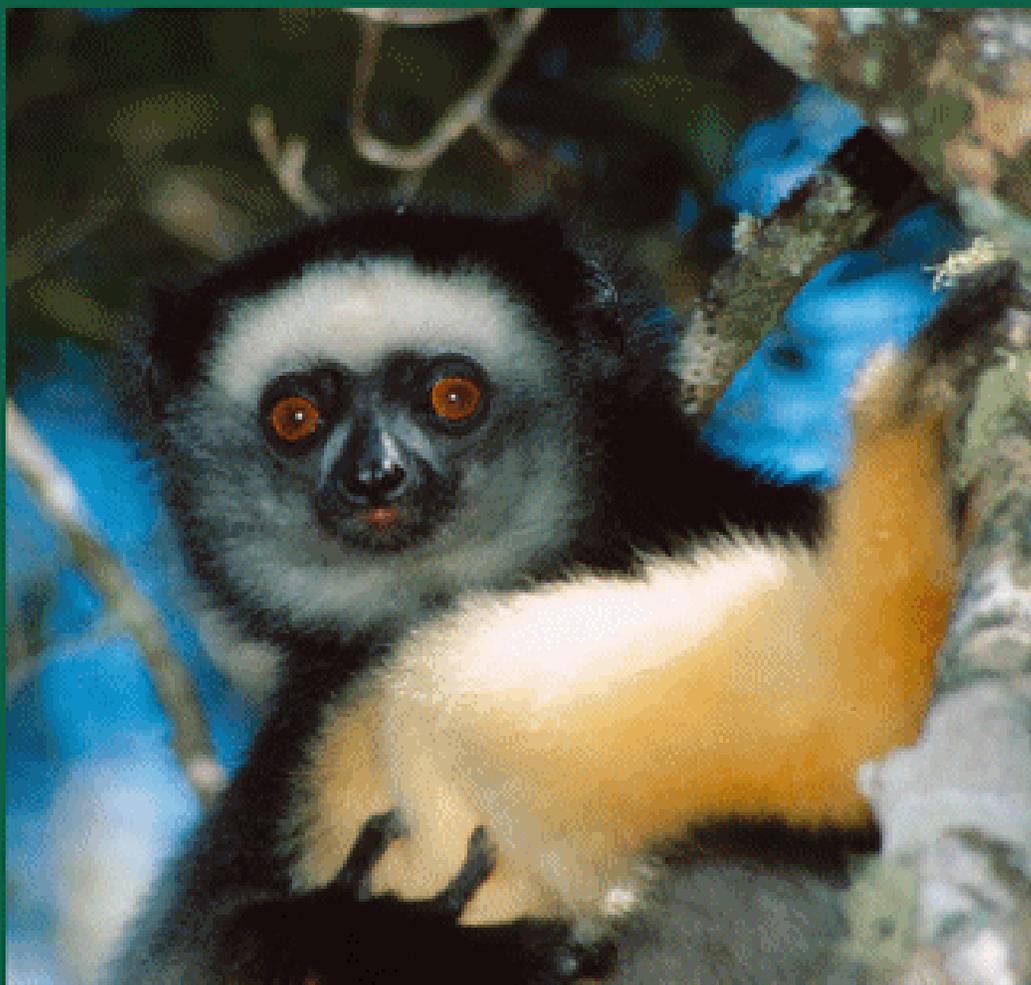


BIOTROPICA

THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Volume 40 • Number 2 • March 2008



The Association for Tropical Biology and Conservation Inc.

Blackwell Publishing, Inc.

March 2008
Volume 40, Issue 2

Cover photo: Diademed sifaka (*Propithecus diadema*) in a degraded forest fragment at Tsinjoarivo, a high-altitude rainforest in eastern central Madagascar. She was a 2-year-old (juvenile) female at the time of the photo in 2003. In early 2005, she was killed by a fossa as part of a predation event that led to the extirpation of sifakas in that particular fragment. See article on page 231 (photo credit: Mitchell Irwin).

Diademed Sifaka (*Propithecus diadema*) Ranging and Habitat Use in Continuous and Fragmented Forest: Higher Density but Lower Viability in Fragments?

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ABSTRACT

The mechanisms through which forest fragmentation threatens the survival of mammal populations remain poorly known, yet knowledge of this process would greatly aid conservation efforts. I investigated ranging behaviors of diademed sifakas (*Propithecus diadema*) in continuous and fragmented forest at Tsinjoarivo, eastern Madagascar, using focal animal observations to examine home range size, daily path length (DPL), and habitat use relative to forest edges over 12 mo. Sifaka groups in forest fragments had home ranges that were 25–50 percent as large as continuous forest groups, and moderately reduced DPLs. Continuous forest groups foraged more than expected near forest edges while fragment groups avoided edges. Fragments have higher population density than continuous forest; however, several lines of evidence suggest that fragment groups' food resources may be denser, but lower quality. Continuous forest groups appear to be energy-maximizers, maintaining large ranges and preferentially feeding in rare fruiting trees found only in continuous forest interiors, while fragment groups appear to be time-minimizers, using small home ranges and primarily feeding on mistletoe (a fallback food in continuous forest). Therefore, the consequences of fragmentation on long-term viability remain unknown; it is possible that the advantage of increased density is outweighed by longer-term demographic challenges, or other threats (*e.g.*, nutrition, health, social behavior, disease). When animals stranded in forest fragments exhibit complex and potentially unpredictable responses, simple ecological proxies (*e.g.*, incidence patterns and density) are probably inadequate in assessing population health and viability. Ecological study and monitoring is essential in judging the viability of fragmented populations.

Abstract in French is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: conservation; daily path length; edge effects; habitat disturbance; habitat fragmentation; home range; Madagascar.

HABITAT LOSS IS ONE OF THE MOST PERVASIVE THREATS TO BIODIVERSITY WORLDWIDE (Laurance *et al.* 2000, Chapman & Peres 2001). While it is relatively easy to monitor the extent and spatial configuration of habitat loss (Green & Sussman 1990, Jorge & Garcia 1997), relationships between habitat loss and species extinctions are complex and poorly understood, partly due to the confounding effects of fragmentation (Fahrig 2003). While it is clear that complete forest loss causes extirpation of forest-dependent species, the viability of populations in fragments is often uncertain, and highly variable among species (Laurance *et al.* 2002). Many authors have demonstrated marked interspecific variation in susceptibility to fragmentation among primates (Tutin *et al.* 1997, Onderdonk & Chapman 2000, Chiarello & de Melo 2001, Ganzhorn *et al.* 2003) and other mammals (Laurance 1991, Goodman & Rakoton-dravony 2000, Nupp & Swihart 2000); consequently, communities in networks of fragments often show nestedness (*i.e.*, some species are consistently among the first lost; Atmar & Patterson 1993).

Usually no simple variables (*e.g.*, diet, body size, home range) adequately explain this interspecific variation. Some authors have suggested that behavioral plasticity (Dehgan 2003), or tolerance of matrix habitat (Laurance 1991) may be more important than static 'species characteristics' in determining fragmentation tolerance. Unfortunately, although many studies have documented the presence and absence of species in fragments through censuses or trapping, fewer studies have directly investigated these animals' ecology and

behavior in fragments (but see: Menon & Poirier 1996, Estrada *et al.* 1999, Tutin 1999, Chapman *et al.* 2006); we therefore know relatively little about animals' ecological responses and compromises in fragments.

This lack of predictive power is probably due, at least in part, to the broad range of effects subsumed within 'forest fragmentation.' Fragmentation affects animals in three ways: (1) direct anthropogenic impacts (*e.g.*, hunting); (2) altered habitat characteristics in fragments; and (3) spatial constraints on ranging and dispersal (Murcia 1995, Fahrig 2003). These processes can ultimately adversely affect genetic diversity and viability of fragmented populations. Because some effects (particularly the third) can act on long timescales, populations may not be at equilibrium (Chapman *et al.* 2003), confounding attempts to predict species persistence in fragments.

An ideal way of assessing the viability of a fragmented population is to follow the fates of known individuals through time; with appropriate data on natality, mortality, and migration, one can calculate population growth rates and conduct population viability analyses (PVAs). However, for animals with slower life histories, such as primates, the amount of time required to collect these data is too long relative to the often-rapid rate of deforestation. Censuses have proved extremely useful in documenting species richness and altered density in fragments or edges (Lehman *et al.* 2006a), but unless repeated over time, they yield few data with which to infer population vital rates. An intermediate approach is to examine individual animals' diet, behavior, and body condition in altered habitats and compare these data with data from intact habitat, to identify behavioral responses to fragmentation and infer links between altered

Received 22 November 2006; revision accepted 5 June 2007.

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behavior and animal health (and therefore potential reproductive output).

One important response that individuals or groups can use to mediate the effects of fragmentation is adjusting their space use (Ims *et al.* 1993); thus, there are several ways in which fragmentation can affect ranging. First, in the short term, habitat reduction may squeeze animals into smaller areas, especially if they are reluctant to accept smaller group size. Second, fragmentation may alter forest structure and composition, thus altering food-resource quality and/or density. As space requirements and ranging depend strongly on resource density and distribution (Milton 1980, Warren & Crompton 1997, Gehring & Swihart 2004), such changes may alter carrying capacity, and affect home range, population density, and competitive regime. Third, habitat structural changes (*e.g.*, changes in the spacing of vertical supports or in the degree of contact between crowns) could affect the cost of locomotion, although this has not been a major avenue of research. Fourth, as within-group feeding competition is one of the primary costs of group living (Janson & Goldsmith 1995, Barton *et al.* 1996, Chapman & Chapman 2000), fragmentation may affect demographic parameters (including optimum group size). Thus, feedback may occur: altered resource distribution affects travel costs and/or competitive regime, which affects group size, which in turn affects travel costs and ranging patterns.

Meta-analyses (Bender *et al.* 1998, Connor *et al.* 2000) have shown that the relationship between population density and fragment area is highly variable among higher taxonomic groups (insects, birds, and mammals), and even varies among species within groups. However, few studies have directly examined fragmentation's effects on range size and overlap for forest-dependent mammals, and most work on this topic comes from studies of non-human primates (but see Koprowski 2005). For some primates, home range size tends to be smaller for fragment-dwelling groups relative to those occupying continuous forest (*Macaca silenus*: Menon & Poirier 1996; *Alouatta* spp.: Estrada *et al.* 1999, 2002; *Colobus guereza*: Onderdonk & Chapman 2000). Sometimes reduced home range is accompanied by smaller group size (*e.g.*, *C. guereza*: Onderdonk & Chapman 2000), while in other cases fragment groups are larger (*e.g.*, *M. silenus*: Menon & Poirier 1996, Umaphathy & Kumar 2000, Singh *et al.* 2002). When density is examined directly, fragments often have higher density than continuous forest (*Cercopithecus cephus*: Tutin *et al.* 1997; *Alouatta* spp.: Estrada *et al.* 1999, 2002; Bicca-Marques 2003; Rodriguez-Toledo *et al.* 2003; *M. silenus*: Singh *et al.* 2002). In contrast to home range and density, little is known about fragmentation's effects on daily path length (DPL) and habitat use. One might expect that groups in smaller fragments travel less, but no effect was found in a meta-analysis of *Alouatta* populations (Bicca-Marques 2003).

Although there is a large and valuable literature on primate abundance at forest edges based on censuses (Lehman *et al.* 2006a, b), no study has quantitatively assessed individual animals' or groups' habitat use relative to forest edges in any primate (*i.e.*, quantifying a preference for edge or interior habitat). Censuses have reported altered density at edges (Lehman *et al.* 2006a), but whenever home ranges are relatively large, it is unclear whether these result

from altered group density or within-group habitat selection. In addition, censuses can be misleading due to differential detectabilities in different habitats. Lehman *et al.* (2006b) showed that lemur species' horizontal sighting distances did not differ between edges and interiors, but other studies do not report these important tests, and differential habitat use in the vertical dimension may still affect detectability when perpendicular distances are identical.

In this paper, I describe the ranging and habitat use of a prosimian primate, the diademed sifaka (*Propithecus diadema*), in continuous and fragmented forest. I ask: (1) Does home range size and population density differ between continuous and fragmented forest? (2) Does DPL differ between continuous and fragmented forest? (3) How is DPL related to dietary, climatic, and abiotic factors? and (4) How do sifakas use their habitat; are edge habitats preferred or avoided?

METHODS

STUDY SITE.—Tsinjoarivo is located 80 km SSE of Antananarivo, atop the escarpment dividing Madagascar's central plateau from the eastern lowlands (Fig. S1). This region contains an unprotected block of central domain mid-altitude rain forest, within a previously continuous corridor between Ranomafana (150 km SSW) and Mantadia (100 km NE) National Parks. The corridor's western half has been fragmented and degraded by settlers from the central plateau, while the eastern half is minimally disturbed (Irwin 2006).

I established two camps at Tsinjoarivo. Mahatsinjo (19°40'56" S, 47°45'28" E, 1590 m asl) is within a network of hilltop and ridgetop forest fragments. Vatateza (19°43'15" S, 47°51'25" E, 1396 m asl), 12 km to the southeast, is within continuous forest, close to settlements near the Onive river. Forest boundaries are maintained as abrupt transitions rather than ecotones (due to farming and grazing right up to edges). Exact penetration distances of edge effects (Murcia 1995) were not quantified but habitat structure was often visibly different in the outer 20–25 m and certain types of edge effects may have completely pervaded the study fragments. For the purposes of this study, 'edge' is operationally defined as the line demarcating the boundary between forest and matrix (rather than as an area of forest adjacent to matrix). I defined 'matrix' as any nonforest habitat; this included cultivated land, grass, and (rarely) secondary forest attaining only 1–2 m height. Fragments' exact ages are unknown but residents indicate they are > 20-yr old; sifaka groups are remnants of a once-continuous population.

Fragments at Mahatsinjo show altered forest structure (reduced tree density, crown volume, and basal area per hectare) and lower tree diversity relative to Vatateza (Irwin 2006). Sifakas are not currently hunted within the study areas; local residents relate that sifakas have been subject to low-level hunting by blowgun in the past, but this has not been observed in the study area since 2000. Rainfall at Vatateza totals 2632 mm, of which 1697 mm (64.5%) falls during the rainy season (December–March). Rainfall at Mahatsinjo is lower, 2008 mm, with 1317 mm (65.6%) falling during the rainy season. Temperature is highest during December–January and lowest in June–August.

STUDY POPULATION.—Tsinjoarivo sifakas are referred to *P. diadema* (Mayor *et al.* 2004), though morphometric and pelage differences suggest they may be a distinct subspecies. They live in small groups (2–6 individuals, excluding infants) containing one adult male, one–two adult females, and up to four immatures. Group size and composition is similar to *P. edwardsi* at Ranomafana (Pochron & Wright 2003) and *P. diadema* at Mantadia (Powzyk 1997).

Four groups were examined: two in continuous forest at Vatateza (CONT1, CONT2), and two in fragments at Mahatsinjo (FRAG1, FRAG2). Group size was similar (CONT1: 6–7, CONT2: 5–6, FRAG1: 4–5, FRAG2: 5), and all groups had two breeding adults (one male, one female) except CONT2 (one male, two females). Most animals were captured; captures were done using the Pneu-dart™ system, using Telazol® at 25 mg/kg body mass (Glander *et al.* 1992). One to two animals per group were radiocollared (Telonics, Mesa, AZ, U.S.A.; weight ≤ 35 g), and others were given colored collars and pendants. All animals could be reliably identified and observed at close distances during the study.

DATA COLLECTION.—Behavioral data were collected between January and December 2003. CONT groups were followed during the first two weeks of each month and FRAG groups were followed during the last two weeks (except June, when observations started on June 14 and the cycle was compressed). Day-long focal animal follows were conducted. Focal animals included only animals > 1.5-yr old in January 2003, and were selected on a rotating basis to equalize sample sizes. As often as possible, focal animals were located in the morning sleep tree.

Data were collected during 651 follows encompassing 6464 hours; for 278 follows, observers recorded positional data using GPS (Garmin GPS 76 with external antenna; typical reported error 5–10 m). Locations were recorded at the beginning and end of days (sleep sites), and every feeding site for which it was possible to obtain a location (90–97%). To prevent intergroup biases related to the spacing of feeding sites, observers also took *ad lib* locations whenever possible, especially during travel.

DATA ANALYSIS.—All GPS locations (sleeping, feeding, and travel) were used to calculate home ranges, using three methods: Minimum Convex Polygon (MCP), 95 percent fixed kernel, and 50 percent fixed kernel (using Animal Movement Analysis v. 2.04; Hooge & Eichenlaub 1997). The MCP home range is the smallest convex polygon fit around all locations; this method is computationally simple, but can overestimate ranges by including unused areas. Kernel methods produce more realistic ranges using a probabilistic model (Worton 1989). The 95 percent kernel range describes the two-dimensional space in which 95 percent of movement is predicted to occur, used here to estimate home range size; the 50 percent kernel range was used to illustrate core areas. Home ranges were manually restricted to forested areas: forest edges were traced in the field by GPS tracking and when home ranges determined by the software (especially minimum convex polygons) extended into nonforest (*e.g.*, when edges had undulations and concavities), nonforest areas were removed.

Group-specific densities were calculated by dividing average group size (excluding infants) or estimated biomass (Irwin *et al.* 2007) by 95 percent kernel home range size. CONT groups' densities are not adjusted for range overlap, which was not quantified in this study (FRAG groups have no overlap). Powzyk (1997) suggested that only the outer 20–100 m of her sifaka groups' ranges overlapped with neighbors, and a similar situation seems plausible here; intergroup encounters were rare, with the only observed encounter ~ 100 m within CONT2's range.

To calculate DPL, I used only follows for which: (1) daily path was recorded completely between morning and evening sleep trees, or (2) data collection started before 0700 h, and the previous night's sleep site was known (total $N = 247$). Only one animal's path per group per day was recorded. The average number of locations per day was 34.4 in CONT groups and 47.6 in FRAG groups. DPL was calculated using ArcGIS 8.0 (ESRI, Redlands, CA, U.S.A.), by connecting GPS locations from the morning sleep site, through feeding and travel locations, to the evening sleep site. Straight lines (ignoring elevation) were used except when animals passed through nonforest; in these cases paths were constrained within forest unless observers had noted movement outside the forest.

I used two methods to investigate predictors of DPL. First, a General Linear Model (SPSS 13.0) was used to predict DPL using one categorical factor (group membership), one continuous diet variable (% of feeding time accounted for by fruit and seeds; Irwin, in press), and two continuous abiotic variables (day length and average temperature, both using monthly averages). 'Day length' was modeled as: $DL = (50 \times \sin((N - 3)/3 \times 90)) + 50$, where N is number of months from winter equinox. Second, multiple linear regressions were used for individual groups with the three continuous variables as predictors. The 'RSearch' function of GenStats 9.0 was used to compare all possible regression models and those with highest Akaike Information Criterion weights are presented.

To investigate habitat use relative to forest edges, I assigned feeding and sleeping locations to 20-m bands representing incremental distances from edges (0–20 m, etc.). Twenty meters was selected as the minimum practical bandwidth because narrower bands would reduce sample sizes and be small relative to typical GPS accuracy (5–10 m). Sleep sites with no GPS data were assigned to bands using trail location data, when available. Sleep site locations were available for 70–85 percent of groups' data-days; feeding locations were available for 87–98 percent of each group's feeding time in days with GPS data collection. As sleep sites were considered independent data points, deviations from expected distributions (using the proportion of home range area falling into each band) were tested using a G -test with Williams's correction (Sokal & Rohlf 1995); bands were combined so that expected cell counts exceeded five. However, because significant temporal autocorrelation was expected for feeding sites, analyses used daily averages rather than individual feeding sites. Binomial tests were used to test whether groups fed more than expected near edges (expected values were based on the proportion of home range in each category), using a null hypothesis that daily follows were equally likely to have spent more or less time than expected in edge habitat.

TABLE 1. Home range and home range-based density estimates for diademed sifaka *Propithecus diadema* study groups.

Group	No. of days	No. of GPS locations	Home range size (ha)			Group size (average)	Approx. biomass (kg)	Density ¹	
			MCP	95% kernel	50% kernel			Individual density (individuals/km ²)	Biomass per km ²
CONT1	69	2329	83.18	72.24	8.56	5.5	25.50	7.61 ²	35.30 ²
CONT2	73	2559	75.98	79.29	13.42	5.5	26.00	6.94 ²	32.79 ²
FRAG1	71	3521	21.22	19.61	3.53	4	17.325	20.40	88.35
FRAG2	65	2948	40.06	36.78	5.86	5	21.98	13.59	59.76

¹Home range-based estimates using 95 percent kernel home range.

²Density estimates for CONT groups are not adjusted for home range overlap, which is not known for this population.

RESULTS

HOME RANGE.—FRAG groups' home range size was smaller, roughly 25 percent (FRAG1) to 50 percent (FRAG2) than observed in CONT groups (Table 1). Thus, population density is higher in fragments (Table 1): assuming minimal range overlap, individual density for FRAG1 is three times higher than that of CONT groups, and biomass/km² is 2.5 times higher. Even given a (generous) 100-m-wide zone of overlap at CONT groups' home range boundaries, ranges would only be reduced by ~21–28 percent, too little to explain the observed difference in density.

HOME RANGE CONFIGURATIONS RELATIVE TO LANDSCAPE.—Group FRAG1 is the sole group in their 24.1-ha fragment, of which they occupied *ca* 85 percent, and most of the unused area was highly disturbed, with discontinuous canopy and thick undergrowth (Fig. 1). FRAG2 used three connected fragments (central: 20.9 ha, north: 12.7 ha, and southeast: 10.5 ha). No other groups lived in these fragments, but one (FRAG3) existed to the west. The central and northern fragments were separated by an oxcart road, and the central and southeastern fragments were separated by a thin corridor of degraded vegetation. Although animals were highly exposed when crossing between fragments, it was done without traveling on the ground. No matrix-crossing by FRAG groups was observed, though one dispersal (by FRAG1's adult male) was inferred in the region in 2005.

CONT1 occupied a range within continuous forest but with considerable edge exposure (Fig. 1). CONT2 had a similar range, with edge exposure and three cleared areas within its range. Both CONT groups had at least one neighboring group; intergroup relationships may thus have an effect on ranging (*e.g.*, if groups actively monitor neighboring groups they may spend more time than expected at range boundaries that fall within forest rather than at edges). FRAG groups' ranges had more edge habitat: the proportion of the range within 40 m of an edge was much higher in fragments (CONT1: 18%; CONT2: 24%; FRAG1: 44%; FRAG2: 70%).

FRAG groups' core areas were distributed in fragment interiors, while CONT1's core areas were concentrated along forest edges (Fig. 1). This group frequently fed on two edge-specific (heliophilic)

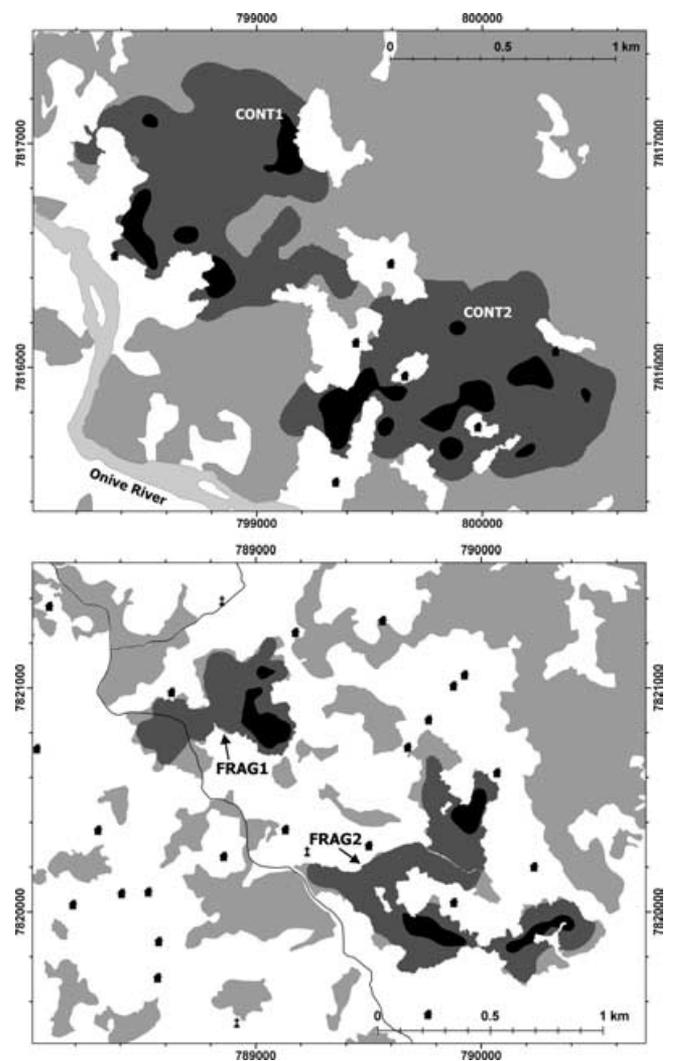


FIGURE 1. Kernel home ranges for *Propithecus diadema* study groups. White: deforested areas, light gray: forest cover, dark gray: 95 percent kernel home ranges, black: 50 percent kernel home ranges (core areas); grid values: UTM coordinates (m).

TABLE 2. Sample size (days), average DPL, standard deviation, and range for four study groups and two sites.

Group	N	Daily path length (m)			Site	N	Daily path length (m)		
		Mean	SD	Range			Mean	SD	Range
CONT1	59	1046	304	431–2014	CONT	125	987	288	412–2014
CONT2	66	935	263	412–1599					
FRAG1	66	769	208	342–1439	FRAG	122	837	218	342–1539
FRAG2	56	917	204	464–1539					

trees (*Solanum mauritianum* and *Maesa lanceolata*) in these areas. Group CONT2 was intermediate, with some core areas near edges and others in the forest interior.

DAILY PATH LENGTH.—Average DPL was slightly shorter for FRAG groups (837 m) than for CONT groups (987 m; Table 2). FRAG1 had the shortest DPL (769 m), while FRAG2 was more similar to CONT groups. Differences between sites and groups are significant, even when data are pooled across months (Fig. 2A; Sites: Mann–

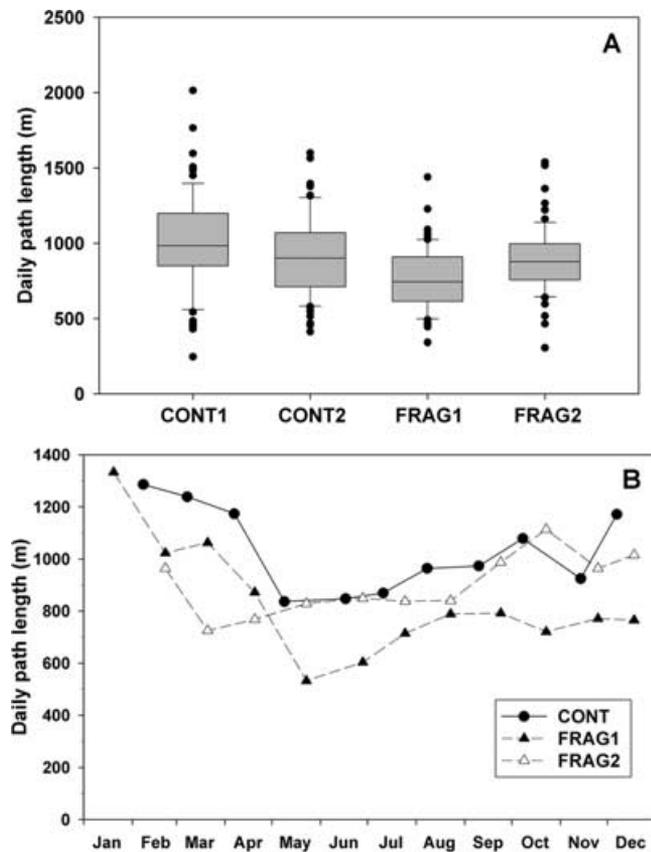


FIGURE 2. (A) Differences among groups in DPL. (B) Seasonal variation in DPL, with CONT groups pooled (due to low sample size in some months).

TABLE 3. General Linear Model predicting log(DPL); adjusted $R^2 = 0.311$; Bold face represents significant factors ($P > 0.05$).

Variable	SS	df	F	P
Corrected Model	1.43	15	8.42	< 0.001
Intercept	40.72	1	3586	< 0.001
Group	0.01	3	0.33	0.806
FR+SD	0.17	1	14.7	< 0.001
DL	0.17	1	15.2	< 0.001
TEMP	0.03	1	2.67	0.104
Group × FR_SD	0.13	3	3.86	0.010
Group × DL	0.026	3	0.78	0.508
Group × TEMP	0.029	3	0.86	0.464
Error	2.62	231		
Total	2142.1	247		
Corrected Total	4.06	246		

Whitney *U* test, $Z = -4.48$, $P < 0.001$; Groups: Kruskal–Wallis ANOVA, $\chi^2 = 35.2$, $P < 0.001$).

Average DPL varied seasonally (Fig. 2B): DPL was highest in January–March (rainy season; when fruit and seeds are emphasized in the diet (Irwin, in press)), and lowest in May–July (early dry season; when leaves are emphasized). FRAG1 consistently had lower DPL than CONT groups (on average, 247 m or 24% less). FRAG2 was intermediate, having low values similar to FRAG1 in some months (e.g., February–April), and higher values similar to CONT groups in others.

PREDICTORS OF DPL.—In the General Linear Model, fruit and seed consumption positively affected DPL, day length positively affected DPL, and temperature had no effect (Table 3). Surprisingly, group membership had no effect on DPL, but the fruit + seed × group interaction term was highly significant, indicating that the relationship between diet and DPL varies among groups. Simple linear regressions show that the relationship between DPL and fruit and seed consumption is positive for all groups except FRAG2 (CONT1: adjusted $R^2 = 0.174$, slope = 6.040; CONT2: adj. $R^2 = 0.239$, slope = 6.102; FRAG1: adj. $R^2 = 0.297$, slope = 5.360; FRAG2: adj. $R^2 = -0.018$, slope = -0.274 ; $P \leq 0.001$ for CONT1, CONT2 and FRAG1, but ns for FRAG2).

The best multiple regression model (highest Akaike Information Criterion weights) varied among groups (Table 4). Fruit + seed consumption entered all models, day length entered three models, and temperature entered only one model. The low AIC weights (0.38–0.67) indicate that there was no overwhelmingly best choice among the possible models.

SPATIAL DISTRIBUTION OF FEEDING TIME.—CONT1’s feeding was concentrated near forest edges; this group spent 43 percent of feeding time within 60 m of an edge, despite the fact that this zone represented only 27 percent of its range. Core areas (Fig. 1) corresponded to clusters of feeding points at the eastern, western, and

TABLE 4. Most appropriate models (highest Akaike weights) for each study group; cell values represent significance values (based on *F*-ratios) for individual predictors in the model.

Group	FR + SD	DL	TEMP	AIC	AIC weight	Adj. R^2
CONT1	0.001	—	—	59.39	0.52	0.174
CONT2	0.001	0.056	—	68	0.40	0.271
FRAG1	< 0.001	0.011	0.028	70	0.67	0.352
FRAG2	0.105	0.001	—	58.41	0.38	0.310

southwestern home range boundaries (Fig. 3A). CONT2 fed less than expected in the outermost edge category, but still spent 44 percent of feeding time within 60 m of an edge (36% of their home range). This pattern is even stronger if one considers additional feeding time spent outside the forest, which was excluded from analyses (feeding on small trees just beyond the edge; CONT1: 5.7 percent of feeding time; CONT2: 1.5%).

In contrast, FRAG groups fed less feeding time than expected within 20 m of the forest edge (FRAG1: 8.8% feeding time vs. 19.6% home range; FRAG2: 27.2% feeding time vs. 36.7% home range), and more in areas farther from the forest edge. Their core areas were in the fragments' centers (Fig. 1), and feeding sites were evenly spread throughout fragments except for the outermost band (Fig. 3B). FRAG groups also fed outside the forest, but not enough to reverse the observed pattern (FRAG1: 0.2% of feeding time; FRAG2: 2.8%).

When daily values were tested, CONT1 fed near forest edges more than expected (Fig. 4) for all three edge categories (0–20 m: $P = 0.027$; 0–40 m: $P = 0.002$; 0–60 m: $P = 0.002$). In contrast, CONT2 fed near edges less than expected for the outermost category ($P = 0.03$), but showed no significant deviation for the other two categories ($P > 0.4$). Both FRAG groups fed less than expected in the 0–20 m band ($P < 0.001$), and FRAG2 fed more than expected in the 0–60 m band ($P = 0.01$).

SPATIAL DISTRIBUTION OF SLEEP SITES.—Although CONT groups fed more than expected near edges, their sleep sites were deeper within the forest. For CONT1, the number of sleep sites within 40 m of an edge was 32 percent lower than expected, but sleep sites at intermediate distances from the edge (between 40 and 80 m) occurred at 220 percent of expected values. Sleeping in deeper forest (> 100 m from an edge) was observed less than expected. The deviation from expected values is significant (*G*-test with William's Correction, $N = 81$, $G_{adj} = 21.0$, $P < 0.001$). Group CONT2's sleep sites, in contrast, follow expected values ($N = 82$, $G_{adj} = 3.4$, $P > 0.5$).

Group FRAG1 shows the most divergent pattern of sleep site selection, strongly preferring the fragment interior ($N = 92$, $G_{adj} = 49.1$, $P < 0.001$). Only 14.1 percent of sleep sites occurred within 40 m of an edge (43.7% of home range area). FRAG2 is intermediate: it avoided edges ($N = 98$, $G_{adj} = 36.5$, $P < 0.001$), but less so than FRAG1.

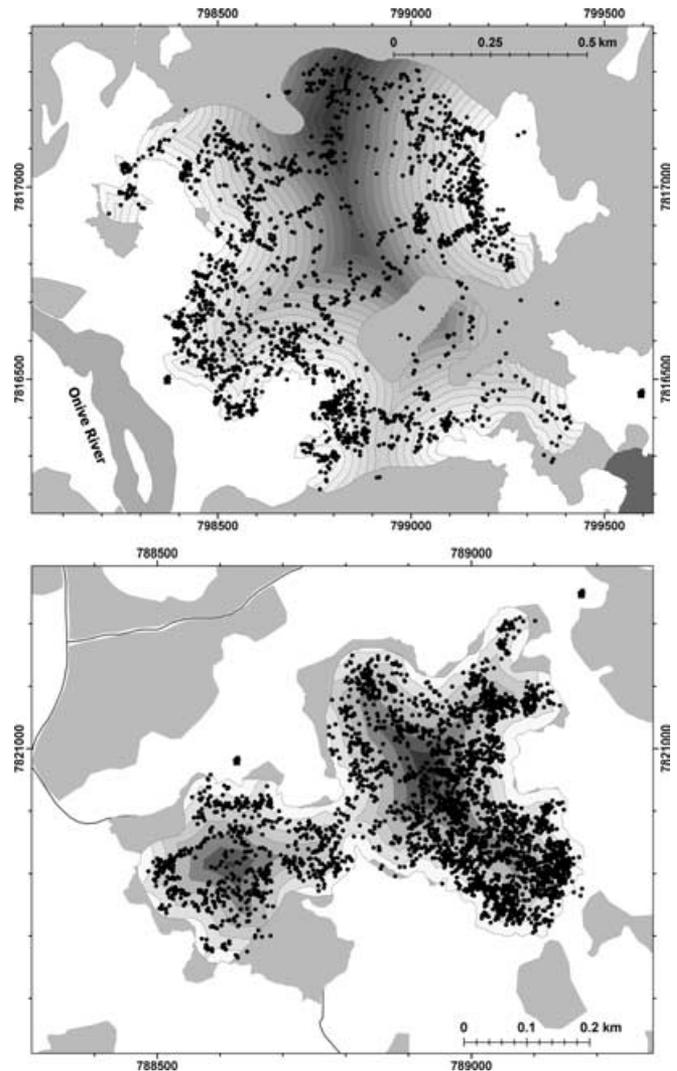


FIGURE 3. Distribution of feeding sites marked by GPS relative to 20-m bands representing proximity to nearest forest edge; groups CONT1 (A) and FRAG1 (B).

DISCUSSION

HOME RANGE SIZE—Sifaka home ranges in fragments were 25–50 percent as large as those in continuous forest. Several factors could cause this situation: (1) physical crowding; (2) reduced predation; (3) reduced emigration ('fence effect': Ostfeld 1994); or (4) altered resource densities. The first three explanations do not adequately explain the difference in range size between CONT and FRAG groups. First, fragment groups leave some parts of fragments unused. The unused portions of FRAG1's fragment are highly disturbed and perhaps unusable (thus, FRAG1 may be subject to crowding), but the northern portion of FRAG2's habitat exhibited very low disturbance, yet was unused. Second, predation rates appear to be higher in fragments (Irwin 2006). Third, reduced emigration should cause larger groups, but group sizes are smaller in fragments. Thus,

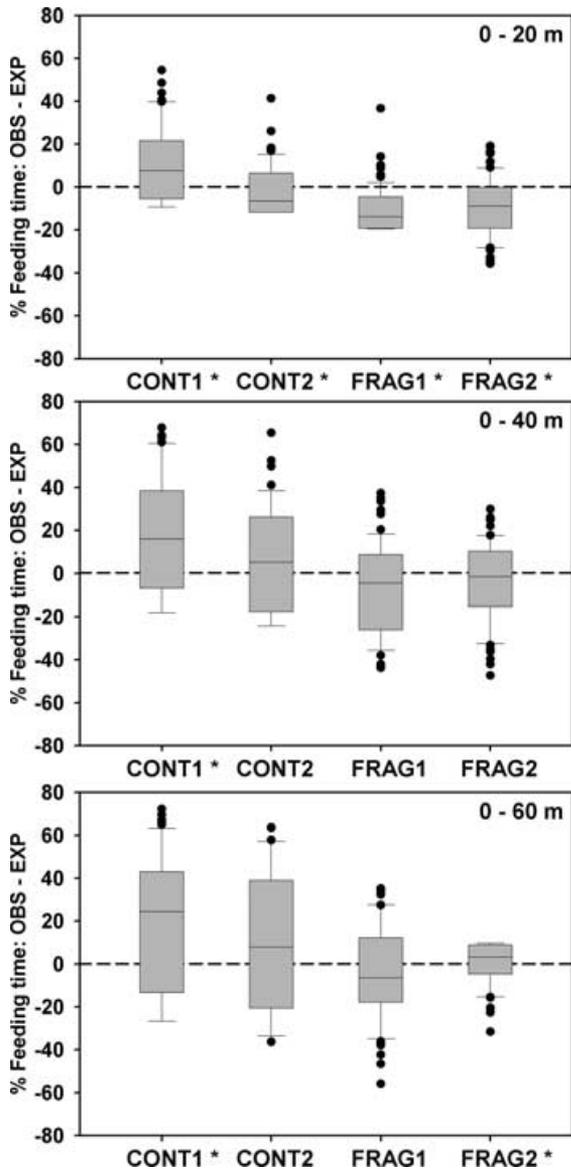


FIGURE 4. Observed minus expected time spent feeding within three edge categories (box plots showing daily values). Asterisks denote significant departures from null hypothesis (equal likelihood of positive and negative values) using binomial test ($\alpha = 0.05$); sample size, CONT1: 53, CONT2: 55, FRAG1: 69, FRAG2: 61.

it is likely that resource distributions play a more important role in determining home range size.

FRAG groups' smaller ranges are consistent with available data on the abundance and distribution of their food resources (Irwin 2007, in press). CONT groups rely on rare, mature fruiting trees of a few species in the rainy season, and use the abundant (99/ha in CONT habitat, 152/ha in FRAG habitat) hemiparasitic mistletoe *Bakerella clavata* as a dry season fallback food (= 'keystone resource' *sensu* Hemingway & Bynum 2005). In contrast, FRAG groups (whose home ranges lack the rare fruit tree species) utilize

the mistletoe as a staple: it is their top food in terms of feeding time throughout most months (FRAG1: 10 of 12 mo, FRAG2: 11 of 12 mo). Thus, I suggest that CONT groups may maintain large ranges to capture enough fruit trees, while FRAG groups graze on the abundant mistletoes in a smaller range. The fact that CONT groups do not simply accept smaller ranges and specialize on mistletoe suggests that the fitness gains of the large range (*i.e.*, nutrient intake) outweigh the costs (*i.e.*, increased travel, intergroup encounters).

DAILY PATH LENGTH.—In contrast to the marked difference in home range size between CONT and FRAG groups, FRAG groups exhibited only moderately shorter DPLs. Furthermore, this difference is consistent with a group size effect, with larger groups (CONT groups; Table 1) ranging farther due to the greater intake requirements of the group as a whole (Janson & Goldsmith 1995); thus the effect of fragmentation *per se* is unclear. The lack of a clear relationship between home range and DPL is consistent with cross-site comparisons: for example, rain forest and dry forest sifakas have similar DPLs despite large home range differences (Wright 1987).

DPL was affected by diet as well as abiotic conditions such as day length and temperature, but there is no overall best predictive model across groups and much of the variation remains unexplained. Diet entered into the best multiple regression model for predicting DPL for all groups, and for all groups except FRAG2, DPL increased with increased fruit and seed consumption.

The lack of a relationship in FRAG2 is hard to explain. This group may be affected by range geometry: while FRAG1's range is relatively round, FRAG2's is more elongate. Elongate, irregular fragments may experience more (and additive) edge effects (Malcolm 1994), constrain the linearity of travel paths (*e.g.*, requiring longer, more convoluted paths than in rounder home ranges), or constrain minimum travel distances for social monitoring (*e.g.*, regular visitation of all home range boundaries). Although some authors have investigated the effects of fragment shape on vegetation (with greater penetration of edge effects in more irregular fragments; Malcolm 1994, Hill & Curran 2005), and species incidence (Martinez-Morales 2005, Anzures-Dadda & Manson 2007), this factor remains understudied relative to fragment size and isolation (especially in terms of its effects on ranging).

USE OF FOREST EDGES.—CONT groups are edge-tolerant: CONT1 fed more than expected near edges, while CONT2 fed more than expected at intermediate edge distances (20–60 m) but avoided the outermost edge. Sleep sites were either distributed throughout the range (CONT2) or concentrated at intermediate edge distances (CONT1; this group may sleep near edges simply because increased feeding near edges makes it likely to end the day near an edge). FRAG groups, in contrast, avoided edges for both feeding and sleeping. FRAG2's tendency to feed more than expected in the 0–60 m band may be an artifact, as 90.3 percent of its range is within this zone. Indeed, it is important to note that FRAG groups' habitat could easily be classified entirely as 'edge'; thus if one defines edge habitat as the area impacted by edge effects, FRAG2 (and perhaps FRAG1) almost certainly occupies 100 percent edge habitat and the question of avoiding or preferring edge habitat becomes moot.

The data presented here suggest that sifakas prefer to feed in moderately disturbed areas of their range. At Tsinjoarivo, continuous forest interiors appear least disturbed, fragment edges appear most disturbed, while edge areas for CONT groups and interior areas for FRAG groups show intermediate disturbance. This preference for moderately disturbed portions of the range may be due to the fact that increased light exposure in these areas increases leaf quality (protein: fiber ratio) or fruit production or because, for CONT groups, higher plant diversity in undisturbed interiors dilutes the density of preferred resources (Lynch & Gonzalez 1993, Ganzhorn 1995, Ganzhorn *et al.* 1997).

ECOLOGICAL STRATEGIES FACILITATING PERSISTENCE IN FRAGMENTS.—Sifakas in fragments survive despite food resource distributions different than those in continuous forest, and demonstrate flexibility in some, but not all, aspects of behavior. Population density is greater, home range size is smaller, and DPL is shorter, while group size and structure remain unchanged. However, indirect evidence suggests FRAG groups may have a lower-quality diet. First, FRAG groups rely on mistletoe year-round, while CONT groups ignore mistletoe in the rainy season in favor of large fruit trees (Irwin, in press). Second, body mass is reduced in fragments (Irwin *et al.* 2007). Third, energetically costly activities (*e.g.*, play) are reduced in fragments (Irwin 2006). This suggests that FRAG groups experience higher *density* of utilized resources, but lower resource *quality*, causing smaller ranges but stressed individuals (Irwin 2007, in press).

CONT groups may be energy-maximizers (Schoener 1971): while they could probably survive in smaller ranges by relying on mistletoes, they maintain large ranges and preferentially feed in rare fruit trees (Irwin, in press). FRAG groups may be time-minimizers: they lack preferred fruit trees, have small ranges, eat mainly mistletoe, avoid energetically expensive activities, and have shorter daily active periods (Irwin, in press). Whether these differences cause reduced viability in fragments is unclear: CONT groups' attraction to edges implies a benefit of edge creation and habitat heterogeneity, but advanced disturbance seems to be disadvantageous. If hunting and forest exploitation can be controlled, sifakas in partially deforested, continuous landscapes may have good chances of survival, but survival of populations in more degraded landscapes, like FRAG groups, remains in question. Further research is necessary, including: (1) nutritional consequences of dietary shifts; (2) consequences of behavioral changes (Irwin 2007); (3) altered prevalence and transmission of diseases and parasites (Gillespie & Chapman 2006); and (4) demographic constraints (*e.g.*, Allee effects, altered reproduction and mortality rates, and constrained dispersal). Any of these factors could cause population decline in fragments, meaning that fragments contain sink populations, or remnant populations headed for extinction.

Finally, it would be useful to explore the generality of these results. The data presented here are cross-sectional (*i.e.*, groups were studied simultaneously in fragmented and continuous habitat); longitudinal study within one area pre- and postfragmentation, though more difficult logistically, would be a more direct test of fragmentation's effects. The two sites were selected to be as close together as

possible and local residents revealed that Mahatsinjo's forest was very similar to Vatateza in species composition and physical structure before fragmentation, but geographic variation (*e.g.*, topography, rainfall) may have contributed to the patterns observed.

IMPLICATIONS FOR CONSERVATION IN FRAGMENTED LANDSCAPES.—This study emphasizes the complex, unpredictable ways in which species may cope with habitat fragmentation, and contributes to our appreciation of the broad interspecific variation seen in fragmentation tolerance. Conservation biologists serious about avoiding extinctions in fragmented landscapes must therefore consider animals' responses to landscape structure in any relevant management plans.

Various tools are available to assess animal population health in forest fragments. These range from analytically ideal but labor-intensive methods (*i.e.*, PVAs based on long-term demographic monitoring of known individuals) to more often-utilized rapid census methodologies. Given the rapid pace of habitat fragmentation, however, estimating the vital rates needed for accurate PVAs via long-term demographic monitoring is impractical for most primate species. Similarly, while there can be no denying the importance of census studies in ecology, as they represent an accessible and analytically sound method of comparing population densities across space and time, researchers must realize the limitations of census data. For example, although it has been acknowledged that population density can be an inappropriate index of habitat quality (van Horne 1983), many studies have failed to consider these warnings (Johns & Skorupa 1987). Most importantly, censuses cannot identify when a disturbed area represents a demographic sink (*i.e.*, a local population sustained by immigration, rather than a viable, self-sustaining population). In the present study, increased sifaka density in fragments is coincident with signs of stress (*e.g.*, reduced body mass), which potentially threatens long-term survival, underscoring the fact that census data are not always sufficient for predicting population viability in habitat fragments.

Few forests in Madagascar (Green & Sussman 1990) or elsewhere in the tropics (Jorge & Garcia 1997, Laurance *et al.* 2001) remain untouched by fragmentation and disturbance; thus we are rapidly losing the luxury of ignoring forest fragments in efforts to preserve natural landscapes and biodiversity. Because fragmentation-related threats act over a long timescale, the possibility of large extinction debts (Cowlishaw 1999) in fragmented landscapes is mounting. Although some animal species may never persist in fragments, a better understanding of the ecology of those species showing tolerance in the short term will increase our ability to assess their long-term viability, and facilitate the development of appropriate management plans.

ACKNOWLEDGMENTS

I thank the Government of Madagascar, CAFF/CORE and the Direction des Eaux et Forêts for research authorization. Methods were approved by Stony Brook University IACUC. For research facilitation, I thank P. Wright, B. Andriamihaja, the Malagasy

Institute for the Conservation of Tropical Environments (MICET), and the Institute for the Conservation of Tropical Environments (ICTE: L. Donovan, F. van Berkum). I am grateful for funding from Margot Marsh Biodiversity Foundation, Primate Conservation, Inc., International Primate Protection League, Stony Brook University, Earth and Space Foundation, and National Geographic Society (to K. Glander) and the support of an NSERC postdoctoral fellowship during manuscript preparation. For data collection assistance, I thank research assistants E. Razanadrakoto, H. Rakotoarimanana, E. Ranaivoson, J. Rakotofanala, C. Randriana- rimanana, F. Ranaivomanana, J.-C. Rakotoniaina, P. Rasabo, K. Parks, T. Anderson, N. Melaschenko, J. Lapoint, E. Hatton, J. Mitchell, J. Anderson, J. Tardi, and M. Ali. Student/colleague J.-L. Raharison provided invaluable assistance in Madagascar, K. Glander aided with animal capture and training, and K. Samonds aided in all stages. Discussions with P. Wright, C. Janson, J. Fleagle, D. Doran-Sheehy, and J. Ganzhorn greatly improved this project, and comments from C. Chapman, W. Jungers, T. Di. Fiore, and three anonymous reviewers improved this manuscript.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Figure S1. Location of study site within Madagascar.

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