

Effect of Habitat Structure on Positional Behavior and Support Use in Three Species of Lemur

MARIAN DAGOSTO

Northwestern University Medical School

and NAYUTA YAMASHITA

University of Hong Kong

ABSTRACT. This study compares locomotor and postural behavior and substrate use of three species of lemur, the diademed sifaka (*Propithecus diadema edwardsi*), the brown lemur (*Eulemur fulvus rufus*), and the red-bellied lemur (*Eulemur rubriventer*) at two different localities within Ranomafana National Park. The object of the study is to see if there are quantitative differences in the behavior of the lemurs or their choice of substrates in forests that have different structural attributes. Analysis of the physical characteristics of the habitat demonstrates that compared to the Talatakely area, the forest at Vatoharanana has a higher proportion of larger, taller trees. The behavior of the lemurs also differs in the two areas: all species leap less and climb and move quadrupedally more at Vatoharanana. All species use small size supports less frequently at Vatoharanana, choosing instead medium size supports (all three species) or tiny supports (*Propithecus* and *E. fulvus*) found in tree crowns and terminal branches. The lemurs prefer (i.e. use more often than would be expected based on abundance) large trees at both sites. At Vatoharanana however, they are more frequently observed higher in trees and in taller trees with greater trunk breadth.

The differences in locomotor behavior are in part due to the fact that at Vatoharanana, more bouts are collected during feeding and foraging than during travel. The relationship between this difference in activity pattern and the structural differences in the two forests, however, is not clear. This study points out the need for longer term field studies of positional behavior and substrate use that incorporate the variety of forest types the subject species inhabit.

Key Words: Positional behavior; Habitat structure; Madagascar; *Eulemur*; *Propithecus*.

INTRODUCTION

In the study of primate positional behavior it is usually desired that the data collected be valid for making inferences about interspecific differences in behavior and ultimately morphology. For practical reasons, field studies are limited in time and space. How well such limited studies capture the potential range of behavior of a species is as yet unknown. Determining the kind and extent of sources of intraspecific variation in behavior is crucial because it is the standard by which we judge the importance (and statistical significance) of interspecific variation.

Positional behavior has already been shown to vary intraspecifically due to age, sex, and season in which observations are made (CROMPTON, 1983, 1984; GEBO, 1992; DORAN, 1992a, 1993; GEBO & CHAPMAN, 1995a; DAGOSTO, 1995). One other potential source of variation in behavior that needs to be more carefully assessed is that due to variation in the structure of the habitat. Several workers have argued that habitat architecture can impose constraints on the positional behavior of primates (RIPLEY, 1967, 1977, 1979). CANT (1992, p. 277) suggested that field studies of positional behavior should control for habitat structure to “avoid the possibility that behavioral differences between species or sexes are artifacts of observing them in different

structural contexts." CROMPTON (1984) needed to carefully analyze his data to see if some of the differences he found in his comparison of two galago species (especially in vertical usage) could be the result of having watched them in different habitats. Positional behavior of captive animals is often quite different from their wild relatives (compare the results of DAGOSTO, 1994, with that of GEBO, 1987, for example), and much of this discrepancy may be due to the limited structural context of the captive habitat. Studies of the same species in different areas sometimes yield quite dissimilar results: compare for example CANT'S (1986) and MITTERMEIER'S (1978) studies of *Ateles geoffroyi* and GEBO'S (1992) and MENDEL'S (1976) studies of *Alouatta palliata*. In these cases, it is difficult to assess the degree to which the differences in behavior are due to differences in habitat structure, since the studies did not directly measure the habitat, and the behavioral attributes were measured using different techniques.

On the other hand, it is clear that primates do not use their habitat randomly (e.g. GAUTIER-HION et al., 1981). Sympatric species select microhabitats that are distinguished on the basis of structural as well as floristic criteria (CHARLES-DOMINIQUE, 1977; HARCOURT & NASH, 1986; GANZHORN, 1989; RODMAN, 1991; MCGRAW, 1996). If primate species are keyed to microhabitats (i.e. they are choosy), one might expect population parameters to be affected by structural differences between habitats (e.g. STALLINGS et al., 1989; MEDLEY, 1993), but perhaps little or no change in behavior. RICHARD (1978, 1979) for example found that the positional behavior of *Propithecus verreauxi* did not differ significantly in her northern and southern study areas despite marked structural differences in these two habitats.

To directly assess the possible effect of habitat structure on positional behavior, the ideal study would compare the same species in two or more structurally different habitats using the same observational techniques (and as far as possible control other potentially complicating factors such as the age-sex composition of study groups, time of day and season in which observations are made, etc.). Several such studies of primate positional behavior exist and the results are contradictory. GEBO and CHAPMAN (1995a) found significant variation in the positional behavior of red colobus monkeys (*Colobus badius*) in different habitats, but like RICHARD'S results for *P. verreauxi* cited above, GARBER and PREUTZ (1995) found little difference due to habitat in *Saguinus mystax*, and MCGRAW (1996) found no differences in locomotor behavior or substrate use in five West African cercopithecoids. DORAN and HUNT (1994) found no significant difference between two populations of *Pan troglodytes schweinfurthii* living in different habitats, but some distinction between the woodland dwelling *P. t. schweinfurthii* and the rain forest dwelling *P. t. verus*. This study will extend the database to include three species of Malagasy lemurs, *Eulemur fulvus*, *Eulemur rubriventer*, and *Propithecus diadema*, which were studied in two areas of Ranomafana National Park (WRIGHT, 1992, 1997). The purpose of this paper is to examine the extent to which differences in structural aspects of the habitat affect positional behavior and support use of these species.

MATERIALS AND METHODS

A study of the positional behavior of two species of the genus lemur, *Eulemur fulvus rufus* and *Eulemur rubriventer*, and one species of indriid, *Propithecus diadema edwardsi*, was conducted at Ranomafana National Park, Madagascar. The study site is located in southeastern Madagascar at 47 degrees E longitude and 21 degrees S latitude. The primates were studied at two different locations within the park. Talatakely is a 4 km² trail system located immediately south of the Namarona River. The rainforest in this area is moderately disturbed because of

selective logging and stands of guava (*Psidium cattleyanum*), an introduced fruit tree, are present. The Vatoharanana study area is located 4 km to the south of Talatakely. The site is slightly higher in elevation, less disturbed by logging, and stands of guava are rare. Other information on the sites including climate data is available in WRIGHT (1995, 1997) and OVERDORFF (1991, 1996). Differences in the structure of these sites were established from 10 50 m×2 m plots measured following GENTRY (1982). Plots were made in areas known to be used by all three species. Because of the montane nature of Ranomafana National Park, plots of ridge tops, slopes, and bottoms were equally represented in the sample for each study area, although the plots within each category were chosen randomly. In each plot, every tree greater than 2.5 cm DBH (diameter at breast height) was measured. The variables assessed were tree height and crown height (measured with a clinometer), diameter at breast height (measured with a DBH tape), crown diameter (CD, distance between furthest branches projected to ground and measured with tape measure), distance to the nearest tree at 5 m height (estimated by eye), and distance from the crown to the nearest tree (estimated by eye). Crown volume was calculated from crown height and radius. Types and sizes of substrates available within the crown were estimated by counting the supports in a small area of the tree and multiplying by an appropriate factor. For the smallest supports (<2.5 cm) this factor was often as high as 200. For this reason, and because branch length was not accounted for, these values must be considered to be only gross estimates.

The positional behavior and support use of two similarly sized (2 kg) species of the family Lemuridae, *Eulemur fulvus rufus* and *Eulemur rubriventer* and the larger indriid (*Propithecus diadema edwardsi*, 5–6 kg) was documented during July to August 1989 and 1990, and March to May 1991. Each species was observed for approximately 200 hours. Data were collected on 10 adult individuals of each *Eulemur* species and 14 adult individuals of *Propithecus*, each of which were uniquely marked with cloth collars and tags or radiocollars (GLANDER et al., 1992). No individual was included in the sample unless there were at least 100 observations of it. Each species and habitat sample included males and females, but in any case there are no statistically significant differences in behavior between the sexes in any of the species. All groups were the subject of previous or current behavioral study and were well habituated to the presence of observers. There were no appreciable differences in the ability to follow or observe primates at the two sites. Data were collected on positional behaviors and substrate use. Positional behavior was studied by following marked focal animals during daylight hours (generally 06:00 to 17:00). The categories of movements and postures used are defined in Table 1. In addition to positional behavior, the size and orientation of the substrate used, structural data on the tree used (DBH, height, crown radius), the location of the animal within the tree (height, quadrant), and correlated activity (feeding, traveling, resting, grooming, etc.) were recorded. The definitions of these categories are also given in Table 1.

Behavior was recorded in two ways. Proportions calculated for locomotor behaviors are based on bouts (FLEAGLE, 1976; see DORAN, 1992b; DAGOSTO, 1994, for more discussion of methods of data collection). In addition to bouts, instantaneous time samples were recorded at 2-min intervals. The data for postures, substrate use, and animal location are based on proportions of time samples, i.e. the percent of time spent in each category. The number of total observations for each data type is given in Table 2.

Differences in positional behavior and support use were tested using procedures discussed in DAGOSTO (1994). For each individual, the number of bouts or time samples of each behavior is tallied and expressed as a proportion of the total number of bouts or time samples in that category. Thus, the sample for each species is the set of these proportional values for the number of

Table 1. Positional behaviors and substrate use.

Locomotion*	
Leaping: A movement in which the hindlimbs are used to propel an animal across a gap.	
Climbing: A movement up or down a strongly oblique or vertical support.	
Quadrupedalism: A movement in which all four limbs move in a regular pattern above a horizontal or oblique support. Includes walking and running.	
Other: Includes bridging, dropping.	
Postures	
Sit: To rest with the hindquarters lowered onto a supporting surface.	
Stand: To maintain an upright position on top of a support with legs extended (on all four limbs or bipedally).	
Vertical cling: The animal grasps a vertical or strongly oblique substrate without supporting any of its weight on other branches.	
Suspension: The animal hangs beneath a support suspended by two or more limbs. In lemurs, the most common suspensory posture is quadrupedal, bipedal, and tripodal (two feet and one hand) postures are also used; bimanual postures are rare.	
Other: Lie.	
Supports used	
Size: Measured in cm: t=very small supports of less than 2.5 cm; the animal usually uses several of these to support itself; s=small, 2.5–10.0 cm; m=medium, 10.0–15.0 cm; l=large >15.0 cm.	
Orientation: Horizontal (0+/-30 degrees); Oblique (30–60); Vertical (90+/-30).	
Location	
Height: Measured in meters above the ground.	
Quadrant: C=crown and terminal branch area; MB=major branch area, near the center of the tree; T=trunk.	
Trees used	
DBH: Diameter at breast height, measured in cm.	
Height: Measured in meters.	
Crown diameter: Measured in meters.	

*Definitions after FLEAGLE & MITTERMEIER (1980).

individuals studied. To test for site differences, an exact randomization test based on the F statistic of ANOVA (EDGINGTON, 1987) was used. Randomization tests do not require distributions to be normal, therefore it is not necessary to employ the arcsine transformation prior to analysis. Significance levels are adjusted using the Bonferroni criterion. Because of small sample sizes the power of these tests is low, therefore both traditionally 'significant' ($p < .05$) and 'nearly significant' ($p = .05 - .10$) values are noted and are considered distinctions between groups in the discussion. Table 3 gives the summary statistics for each species and the results of statistical tests.

Table 2. Number of observations for each species in each habitat.

	<i>Propithecus diadema</i>		<i>Eulemur rubriventer</i>		<i>Eulemur fulvus</i>	
	T	V	T	V	T	V
Locomotion	4516	1180	3577	1681	3050	1021
Posture	3100	883	2591	2726	2589	1313
Support size & orientation	2969	796	2572	2551	2527	1491
Quadrant	2803	860	2495	2687	2432	1451
Height animal	2193	810	2502	1973	2369	378
Height tree	1782	752	1623	2235	1849	1001
DBH tree	2014	786	1844	2014	1959	619
CD tree	1389	641	1323	1744	1441	604

The number of animals studied is given in Table 3. T: Talataky; V: Vatoharanana. Locomotor behavior is based on number of bouts; postures, support, and location data are based on 2-min instantaneous time samples.

Table 3. Comparison of positional behavior and substrate use in lemur species at two different areas of Ranomafana National Park, Talatakelly (T) and Vatoharanana (V).

Species	<i>Propithecus diadema</i>		<i>Eulemur rubriventer</i>		<i>Eulemur fulvus</i>	
	T	V	T	V	T	V
Site						
<i>N</i>	9	5	6	4	5	5
Locomotion						
Leap	88.8	85.2**	64.3	58.6	67.7	44.2**
Climb	8.8	9.4	11.7	15.1	8.6	17.1**
Quad	0.6	1.9**	22.5	23.8	22.2	35.6
Other	1.8	2.3	1.8	3.7	3.0	3.1
Posture						
Sit	76.5	84.1*	84.7	70.4*	74.6	96.6**
Stand	.5	0.1*	11.3	4.9	5.5	1.6
Susp	3.3	1.8	0.0	0.1	0.0	0.0
VC	19.0	12.7**	2.8	4.3	1.4	1.4
Other	.5	1.3	1.2	20.4*	18.2	0.4*
Support orientation						
H	42.3	46.1	64.9	75.5	60.4	81.6
O	32.9	32.5	31.9	20.6	37.5	10.8**
V	24.9	21.4	3.2	3.9	2.0	7.6
Support size						
t	7.2	14.8**	23.0	17.6	10.1	36.1*
s	79.1	69.8*	74.8	50.9*	71.5	49.2*
m	10.1	12.9	1.8	25.0**	11.1	12.7**
l	3.6	2.5	0.0	6.5	7.3	2.1
Quadrant						
C	29.1	36.5	21.3	29.3	15.1	64.6**
MB	55.1	53.9	76.8	65.5	83.1	34.0**
T	15.8	9.6	1.9	5.2	1.8	1.4
Height animal (m)						
0–5	14.0	3.6*	5.8	11.5	5.5	4.8
5–10	40.5	9.6*	39.3	15.7	47.3	2.7*
10–15	17.9	18.5	36.8	12.0	30.5	16.8
15–20	11.7	26.4*	10.5	36.9*	15.4	26.2
20–25	14.2	26.2	7.6	19.3	1.3	39.7*
>25	0.6	15.7	0.0	4.7	0.0	9.7
Height tree (m)						
0–5	0.6	1.0	0.4	6.9*	0.0	4.9*
5–10	21.3	8.8	12.7	8.4	14.3	3.4*
10–15	24.5	24.4	51.7	12.8	49.3	20.3
15–20	26.2	17.5	29.4	16.0	29.4	23.1
20–25	25.9	24.3	5.8	35.0*	5.4	36.2
>25	1.4	23.9*	0.0	20.8	1.5	12.1
DBH tree (cm)						
0–10	7.5	5.8	10.5	7.0	5.8	0.0
11–20	48.1	21.3	34.9	31.7	44.9	5.2*
21–30	26.3	17.5	34.1	10.9	22.2	42.7
31–45	8.8	28.7	6.0	22.7	24.5	24.2
46–60	6.2	7.2	14.4	10.7	1.1	22.4
>60	3.0	19.6	0.1	17.0	1.4	5.5
CD tree (m)						
0–3	43.2	15.3*	33.4	20.6	29.5	.9*
4–6	24.2	18.9	42.6	14.6	39.9	12.3
7–10	29.9	48.1	22.3	49.3	24.1	50.1
11–15	2.6	17.6*	1.4	10.9**	4.2	28.7
15–20	0.0	0.1	0.0	4.7	2.3	.5
>20	0.0	0.0	0.0	0.0	0.0	7.4

The number reported for each species is the mean of the proportions (expressed as %) calculated for each individual. *N* is the number of individuals studied at each site. Comparisons with *p* values of .05–.10 are marked with one asterisk; those with *p* values <.05 are marked with two asterisks. See Table 1 for the abbreviation.

RESULTS

STRUCTURAL CHARACTERISTICS OF THE HABITAT

The forests at Talatakely and Vatoharanana proved to be structurally different, a conclusion also reached by WHITE *et al.* (1995) from a much larger sample of trees. Small trees dominate both forests, but the trees at Vatoharanana have greater mean DBH (13.5 cm vs 10.0 cm, $p < .01$, Mann-Whitney *U*-test) and crown volumes (24.4 vs 11.5, $p < .04$). When classed into size categories (Fig. 1A, 1B) the distributions are also significantly different with Vatoharanana having a greater proportion of large trees (for DBH, $G = 24.86$, $p < .005$; for CV, $G = 14.41$, $p < .05$). The mean height of trees is also greater at Vatoharanana (10.4 m vs 9.6 m), but this difference is not statistically significant. However, the distribution of trees does indicate a small but significantly higher proportion of tall trees (>15 m) at Vatoharanana ($G = 15.86$, $p < .01$) (Fig. 1C). The distance between trees below the crown (at 5 m) is not different, but at the level of the crown, Vatoharanana has a significantly higher proportion of trees for which the distance to the next tree is greater than 5 m (lemurs rarely make leaps greater than 3 m) ($G = 43.18$, $p < .005$) (Fig. 1D). The tree crowns at Talatakely have a higher proportion of horizontal supports ($G = 424.68$, $p < .001$) (Fig. 1E) and fewer large supports ($G = 519.283$, $p < .001$) (Fig. 1F).

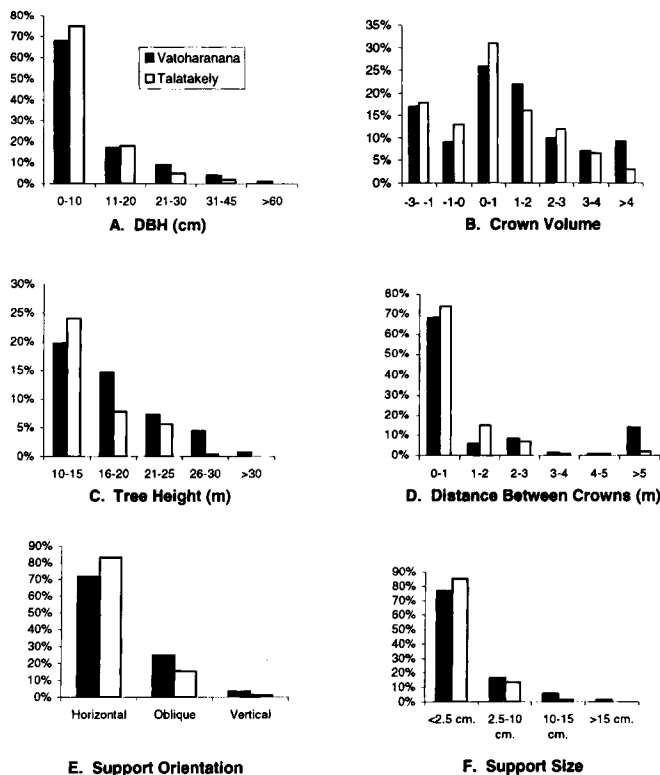


Fig. 1. Comparison of distributions of structural characteristics of trees at Talatakely (white bars) and Vatoharanana (black bars). **A.** Diameter at breast height; **B.** log crown volume; **C.** tree height; **D.** distance between crowns of trees; **E.** support orientation; **F.** support size.

LOCOMOTION AND POSTURE

Each species shows a similar response to the different habitats, but varies in its degree. *Eulemur fulvus* shows the strongest difference, with leaping being much less frequent at Vatoharanana (44%) than at Talatakely (68%), and climbing more frequent at Vatoharanana (17% vs 9%; Table 3). Quadrupedalism is more frequent at Vatoharanana (36% vs 22%), although not significantly so. The same pattern holds for *Eulemur rubriventer*, but the differences are not marked enough to be statistically significant. Although the magnitude of the difference is much less, a similar pattern is true for *Propithecus diadema*: the proportions of leaping and quadrupedalism are significantly different at the two sites.

There were only two differences in postures used significant at the 5% level: *Eulemur fulvus* spends more time sitting at Vatoharanana, and *Propithecus diadema* spends more time vertical clinging at Talatakely.

SUPPORTS USED

Eulemur uses medium supports more often and small supports less often at Vatoharanana. *P. diadema* and *E. fulvus* use the 't' class of supports (which represents the terminal branch area) more often at Vatoharanana at the expense of small supports which are used less often. The only significant difference in the orientation of supports used is in *E. fulvus*, which uses oblique supports more often at Talatakely.

LOCATION

The differences in support size use are probably related to the fact that at Talatakely, *E. fulvus* uses the crown and terminal branch area (in which the very smallest supports are most common) less often than at Vatoharanana (Table 3). This is also true of *Propithecus*, but the difference is less extreme in magnitude and is not statistically significant.

As expected from the greater number of tall trees at Vatoharanana, the primates were observed at greater heights more often at this site than at Talatakely. At Talatakely, all species are observed at 0–15 m more than 70% of the time, whereas at Vatoharanana, they are observed at 15–25 m more than 60% of the time (Table 3).

STRUCTURAL CHARACTERISTICS OF TREES USED

The characteristics of the trees used generally parallel expectations given the structural differences in the two sites. Thus, the primates were more commonly observed in taller trees with greater DBH at Vatoharanana. For all three species, more than 65% of trees used at Vatoharanana are greater than 15 m in height, whereas at Talatakely more than 45% of trees used are less than 15 m in height. Similarly, for all three species 50% of the trees used at Vatoharanana have a DBH greater than 30 cm but only 20–30% of trees used at Talatakely are this large. There is no significant correlation of the ranks of different height and DBH classes for any of the species at the two sites (Spearman's $\rho < .3$ in all species). Sixteen–37% of trees used at Vatoharanana have crown diameters greater than 10 m, but at Talatakely less than 7% of trees used are this large. Although all species used trees of larger crown diameter more often at Vatoharanana, the difference in ranks of classes is only insignificant for *E. fulvus* ($\rho = .086$ vs $.971$ in *P. diadema* and $.771$ in *E. rubriventer*) (Table 3).

INTERPRETATION OF RESULTS

Positional behavior and substrate use of lemurs differs at sites that are structurally distinct. The degree of response varied, with *E. fulvus* showing the greatest differentiation, *Propithecus* a small, but statistically significant difference and *E. rubriventer* a moderate, but not significant difference. Some distinctions, such as structural characteristics of trees used and heights animals were observed at, reflect expectations based on differences between the habitats. Both *Eulemur* species and *Propithecus* took advantage of the larger trees that are available at Vatoharanana. This is true for overall activity (Table 3) and if only trees used in feeding or foraging are examined (Table 4). The differences in locomotion may be related to this. For all three species, leaping is less frequent and quadrupedalism more frequent at Vatoharanana, the site with the greater proportion of large trees. All species also spent more time foraging and feeding at Vatoharanana and as a result bouts collected during feeding make a larger contribution to total bouts at this site (Table 5). In New and Old World monkeys, movement within a tree while feeding and foraging differs from that during travel (movement between trees) and from overall locomotor patterns: leaping is less frequent and quadrupedalism and climbing are more frequent (FLEAGLE & MITTERMEIER, 1980; GEB0, 1992; GEB0 & CHAPMAN, 1995b). The same is true for Malagasy lemurs (Table 6). Thus, the lower frequencies of leaping at Vatoharanana partly reflect differences in time engaged in feeding/foraging vs travel. Larger food trees can

Table 4. Comparison of tree characteristics of trees used during feeding and foraging activity at Talatakey and Vatoharanana.

Species Site	<i>Propithecus diadema</i>		<i>Eulemur rubriventer</i>		<i>Eulemur fulvus</i>	
	T	V	T	V	T	V
Quadrant						
C	60.1	70.4	54.6	67.1	64.5	89.1*
MB	23.0	17.8	38.9	19.0*	26.4	7.4
T	16.8	9.9	6.3	13.6	6.9	0.0*
Height tree (m)						
0-5	2.1	.6	1.7	18.0**	0.0	7.7
5-10	14.0	2.8*	18.0	5.8	38.6	4.5*
10-15	23.5	7.5	40.8	18.7	39.7	9.2*
15-20	21.9	32.4	27.1	28.5	17.4	7.6
20-25	35.3	34.7	12.3	25.0	4.2	47.9**
>25	3.1	22.0**	0.2	3.9	0.0	23.1*
DBH tree (cm)						
0-10	15.6	2.1	23.5	17.4	34.6	0.0**
11-20	39.5	20.1	38.0	33.5	32.7	6.7*
21-30	21.9	28.4	16.1	11.6	13.4	39.7
31-45	6.3	29.3**	10.8	22.1	11.4	33.1
46-60	7.9	6.5	11.1	3.0	6.4	20.5
>60	8.7	13.7	.6	12.5**	0.0	0.0
CD tree (m)						
0-3	37.2	12.3*	24.2	33.4	65.9	4.7**
4-6	34.7	28.6	46.5	27.1	15.1	12.8
7-10	24.3	50.6	18.9	36.0	15.7	57.6*
11-15	3.7	8.5	9.0	1.1	3.3	22.9
15-20	0.0	0.0	1.0	2.3	0.0	2.0
>20	0.0	0.0	0.3	0.0	0.0	0.0

See Tables 1 and 3 for the abbreviation and caption.

provide an opportunity to spend more time in a single food patch and less time moving between patches (WRIGHT, 1986; STRIER, 1987). OVERDORFF (1991, 1993), however, found that patch size does not correlate with daily travel distance of *Eulemur* at Vatoharanana. Rather, travel distance (and thus presumably time spent traveling) correlates positively with dietary diversity and number of patches visited. These variables were not measured at Talatakely, so it cannot be determined if intersite differences in these factors are present. There is also a higher proportion of large, unbridgeable discontinuities between the crowns of large trees at Vatoharanana than at Talatakely (Fig. 1D). Lemurs may thus be forced to spend more effort moving within crowns to locate manageable travel paths.

Difference in activity pattern fails to account fully for the intersite differences observed in *E. fulvus*. In *E. rubriventer* and *P. diadema* there is no difference between sites in the proportions

Table 5. Proportions of time spent in two activities, Travel and Feeding/Foraging, based on time samples and bouts, at two different areas of Ranomafana National Park Talatakely (T) and Vatoharanana (V).

Species	Site	Time samples		Bouts		T/F
		%travel	%feed	%travel	%feed	
<i>E. rubriventer</i>	T	9.9	16.8	49.8	30.3	1.7
	V	4.1	27.3	32.6	45.9	0.7
<i>E. fulvus</i>	T	6.5	11.3	43.3	37.8	1.2
	V	6.7	36.5	41.2	42.0	1.0
<i>P. diadema</i>	T	10.1	36.6	57.7	24.2	2.4
	V	9.7	36.1	61.2	27.1	2.3

In the time samples column, the number represents the proportion of the total number of time samples devoted to travel (%travel) and feeding/foraging (%feed). In the bouts column, the number represents the proportion of bouts derived from travel (%travel) and feeding/foraging (%feed). T/F is the proportion of travel bouts to feeding bouts. Compared to Talatakely, at Vatoharanana a greater proportion of bouts derives from observations during feeding.

Table 6. Proportions of different locomotor behaviors in two different behavioral contexts: Traveling (movement between food trees or resting trees) and Feeding (movement within a food patch).

	<i>P. diadema</i>			<i>E. rubriventer</i>			<i>E. fulvus</i>		
	Travel	Feed	<i>p</i>	Travel	Feed	<i>p</i>	Travel	Feed	<i>p</i>
Talatakely									
Leap	93.5	67.4	**	68.8	50.2	**	74.0	51.7	**
Climb	5.3	23.4	**	11.8	16.6	ns	8.1	12.8	**
Quad	0.2	3.5	**	13.8	31.1	**	16.4	31.1	**
Other	1.0	5.8	**	1.5	1.9	ns	1.4	4.3	ns
Vatoharanana									
Leap	90.1	64.8	*	64.1	50.7	*	52.0	30.1	**
Climb	7.4	26.2	**	16.5	16.0	ns	19.0	15.1	ns
Quad	0.1	4.3	ns	17.5	29.4	*	27.0	50.4	**
Other	1.4	4.7	ns	1.9	3.9	**	2.6	4.4	ns

Intersite comparison									
Leap	*	ns		ns	ns		**	**	
Climb	ns	ns		*	ns		**	ns	
Quad	ns	ns		ns	ns		**	**	
Other	ns	ns		ns	ns		ns	ns	

The number reported for each species is the mean of frequencies calculated for each individual studied. *p* values are for the comparison of behavior during travel with behavior during feeding within each site, see Table 3. Most contrasts are significantly different in all three species at both sites. The "intersite comparison" contrasts behavior between Talatakely and Vatoharanana controlling for behavioral context (i.e. leaping during travel at Vatoharanana vs leaping during travel at Talatakely). *P. diadema* and *E. rubriventer* show few intersite differences; in *E. fulvus*, however, behavior is different at the two sites in both behavioral contexts.

Table 7. The five most frequently eaten foods as determined by percent time spent feeding on or foraging for each food.

	Vatoharanana (dry+wet)		Talatakely 90 (dry)		Talatakely 91 (wet)	
<i>Propithecus diadema</i>	Rotra (Myrtaceae)	49	Rahiaka	46	Guava (Myrtaceae)	63
	Rahiaka (Sapotaceae)	25	Rotra	25	Rahiaka	10
	Sandrany (Anacardiaceae)	7	Vahiambanikondro (Apocynaceae)	13	Rotra	7
	Kalifana (Myrsinaceae)	4	Vomboana (Leguminosae)	5	Kalafambakaka (Myrsinaceae)	5
	Tongolahy (Loranathaceae)	3	Fatsikahitra (Rubiaceae)	3	Tongolahy	3
<i>Eulemur rubriventer</i>	Harongana (Hypericoidea)	26	Tavolopiana (Lauraceae)	16	Guava	60
	Fohaninanity (Rubiaceae)	17	Kalifana	13	Roindambo (Smilacaceae)	14
	Kalifana	12	Tavolo	13	Amboralahy (Monimiaceae)	7
	Unid. leaves	11	Fatsikahitra	11	Kalafambakaka	5
	Rahiaka	10	Maka (Cunoniaceae)	11	Nonoka (Moraceae)	5
<i>Eulemur fulvus</i>	Harongana	69	Guava	31	Guava	77
	Sandrany	13	Lanary madinkia (Sapindaceae)	12	Nonoka	4
	Unid. leaves	7	Malanimata	10	Vahimboimena	3
	Nonoka	5	Ravinala (Strelitziaceae)	10	Vomboana	3
	Kalifana	2	Tavolo	9	Tongolahy	2

of behavior during travel or feeding (i.e. travel at Talatakely does not differ from travel at Vatoharanana; see the “Intersite comparison” of Table 6); thus the difference in overall (all behavioral contexts) locomotor behavior between sites is likely due to intersite difference in the proportion of bouts derived from feeding and travel, as argued above. In contrast, in *E. fulvus*, there is a difference not only in the proportion of bouts derived from feeding vs travel, but also significant intersite differences in locomotor behavior during both travel and feeding (i.e. the proportion of leaping during travel is less frequent at Vatoharanana than at Talatakely; Table 6). The reason for this difference in behavior is unclear.

The contrast between sites in both locomotor behavior and in tree location is greatest for *Eulemur fulvus*, which also spent much less time in the canopy and terminal branch milieu and used trees of smaller crown diameter at Talatakely. Perhaps one reason for this distinction between *E. fulvus* and the other species has to do with resource use. *E. fulvus* at Talatakely relied heavily on the introduced guava (which occurs in stands of small, short trees) during both observation periods (July–August 1990 and March–May 1991) in contrast to *E. rubriventer* and *Propithecus* which only used this resource during part of the study period (March–April 1991) (Table 7). Because the guava trees are small, the brown lemurs didn’t always enter the crown quadrant (where quadrupedal movement is most often employed), but harvested fruits from small or medium sized supports in the “major branch” area below the crown (where leaping is frequently employed to move between large branches and trunks).

The data compared here combines observations collected during two different time periods: a drier, cooler season (July–August) and a warmer, wetter season (March–May). Do site-specific differences in positional behavior still exist when these seasonal differences are controlled for? Table 8 breaks the data down in this fashion. Each comparison with the exception of the *P. diadema* dry season sample still reveals significant (*E. fulvus*, *P. diadema* wet season) or potentially significant (*E. rubriventer*: the number of individuals in these samples is too small to allow statistical testing, but the magnitude of the differences is relatively large) site specific differences in locomotor behavior, but not always in the same direction as the combined sample. For example, the *E. fulvus* (dry season), *E. rubriventer* (dry season), and *P. diadema* (wet season) samples reflect the overall trend of a greater proportion of leaping at the Talatakely site, but the *E. rubriventer* wet season sample shows the opposite condition. Whether

Table 8. Comparison of proportions of locomotor behaviors at two different areas of Ranomafana National Park by season.

Season	Site	Dry season		Wet season	
		T	V	T	V
<i>Propithecus diadema</i>	Leap	87.8	91.4	89.5	85.4*
	Climb	9.7	6.4	8.6	9.8**
	Quad	0.7	1.3*	0.4	2.1*
	Other	1.8	0.9	1.7	2.6
<i>Eulemur rubriventer</i>	Leap	69.3	53.5	59.7	64.0
	Climb	12.7	15.5	11.3	15.5
	Quad	18.0	27.5	27.3	20.0
	Other	0.7	4.0	2.0	1.0
<i>Eulemur fulvus</i>	Leap	73.3	44.2**	62.7	nd
	Climb	7.1	17.2**	8.5	nd
	Quad	18.9	35.4**	25.8	nd
	Other	0.7	3.0*	2.0	nd

The dry season data are from July to August, the wet season data are from March to May (see DAGOSTO, 1995 for more details). Comparisons with p values from .05–.10 are marked with one asterisk, those with p values <.05 with two asterisks. nd: insufficient data.

such seasonal variation at both sites would eventually “wash out” the overall site-specific differences in positional behavior discussed here can only be addressed by a longer term study given that at Ranomafana the production of food is variable from year to year, and many important resources may fruit biennially (OVERDORFF, 1991).

The Talatakely data is complicated by that fact that at this site all three species ate guava, an introduced species, quite extensively during the March–May observation period. Therefore, intersite variation may be due primarily to use of this resource (and its particular structural characteristics), and thus could be an artifact. Would similar differences in behavior exist if only indigenous foods were eaten at Talatakely? The dry season data for *Eulemur rubriventer* also shows a large magnitude of intersite difference in locomotor behavior, even though this species did not utilize any introduced resources at either locality.

DISCUSSION

These data indicate that the positional behavior and support usage of lemurs is flexible enough to respond to differences in habitat architecture, especially as these are related to the structure of food trees and the location and distribution of food items in time and space. At worst, the differences observed demonstrate only stochastic variation in behavior. Intraspecific behavioral variation needs to be recognized by morphologists attempting to explain anatomical distinctions. If this study had been conducted at only one of these sites, very different stories would have emerged. One would have concluded from the Vatoharanana data that positional behavior of *E. fulvus* and *E. rubriventer* was significantly different, with the latter species engaging in more leaping and less quadrupedalism associated with its greater use of the major branch region, but from the Talatakely data that *E. rubriventer* leapt slightly less and climbed more than *E. fulvus*, and showed no differences in quadrant use. Sampling behavior from different areas of a species' habitat and in different seasons is necessary to gain a better appreciation of behavioral range especially for primate species that inhabit a variety of different habitat types and/or live in very seasonal climates.

It is also clear that lemurs are not using supports and trees simply based on their availability. For all three species at both sites, trees used differ from those available in terms of height, DBH, and crown diameter (all comparisons with G -test at $p < .05$ or less, except *E. rubriventer* crown diameter at Talatakelly). Lemurs tend to use large trees more often than they are represented at both sites; this is also reflected in their choice of larger than available food patches at Vatoharanana (OVERDORFF, 1991). Preference for relatively large trees (for both food resources and sleeping sites) has also been documented by others for *Varecia* (WHITE et al., 1995) and in other primate species (e.g. GAUTIER-HION et al., 1981; SA & STRIER, 1992; MEDLEY, 1993).

The results of this study agree with previously documented intraspecific variation associated with habitat differences (GEBO & CHAPMAN, 1995a), but contrast with other studies which show little variation in behavior despite differences in the structure of the habitat (GARBER & PREUTZ, 1995; MCGRAW, 1996). There are several possible reasons for this discrepancy. It is conceivable that there are differences in species' ability to respond: some may be more constrained than others, and there may be no rule about the presence or degree of response to change. For example, although the locomotor behavior of each of the three lemur species altered in a similar direction, they differed in the degree of change. There may also be differences in the amount of habitat contrast in these studies (MCGRAW, 1996); there is as yet no standard way of measuring or analyzing habitat so the studies cannot be directly compared. We also have little idea what features of habitat matter most to primates: both structural attributes like support sizes and orientations, support density, size of trees, gaps between trees, and nonstructural attributes like the size, spacing, and diversity of resource patches may impact positional behavior. Not all of these variables are measured in all of the studies. There are also differences among the studies in the scale at which differences are detected. Those who find no differences are usually looking at a large scale: rank order of behaviors (GARBER & PREUTZ, 1995) or tests of the whole behavioral repertoire (DORAN & HUNT, 1994; MCGRAW, 1996). Those who have found differences are looking at a smaller scale: differences in the frequency of specific behaviors (GEBO & CHAPMAN, 1995a; this paper). In any case, it is obvious that more work needs to be done to clarify this issue.

Acknowledgements. The work here could not have been accomplished without the generous and capable assistance of many people particularly Dr. PATRICIA WRIGHT (Director of RNP), Mme. BERTHE RAKOTOSAMIMANANA (Ministry of Education, Madagascar), the Department d'Eaux et Forêts, Madagascar, Dr. FRANCES WHITE, Dr. DEBORAH OVERDORFF, and Dr. ADINA MERENLENDER. A very special thank goes to the research guides of RNP: RAJERARISON, EMILE; RAKOTO, RAPHAEL; RAKOTONIRINA, GEORGES; RAKOTONIRINA, PAUL; RAKOTONIRINA, WILLIAUME; RANDRIAMAMPIONONA, RICHARD; RASABO, LORET; TALATA, PIERRE; and TELO, ALBERT. NSF BNS 90-08545 and Northwestern University's Research Grants Committee funded the work.

REFERENCES

- CANT, J. G. H. 1986. Locomotion and feeding postures of spider and howling monkeys: field study and evolutionary interpretation. *Folia Primatol.*, 46: 1–14.
- CANT, J. G. H. 1992. Positional behavior and body size of arboreal primates: a theoretical framework for field studies and an illustration of its application. *Amer. J. Phys. Anthropol.*, 88: 273–283.
- CHARLES-DOMINIQUE, P. 1977. *Ecology and Behavior of Nocturnal Primates*. Columbia Univ. Press, New York.
- CROMPTON, R. H. 1983. Age differences in locomotion of two subtropical Galaginae. *Primates*, 24: 241–259.

- CROMPTON, R. H. 1984. Foraging, habitat structure, and locomotion in two species of *Galago*. In: *Adaptations for Foraging in Nonhuman Primates*, RODMAN, P.; CANT, J. (eds.), Columbia Univ. Press, New York, pp. 73–111.
- DAGOSTO, M. 1994. Testing positional behavior of Malagasy lemurs: a randomization approach. *Amer. J. Phys. Anthropol.*, 94: 189–202.
- DAGOSTO, M. 1995. Seasonal variation in positional behavior of Malagasy lemurs. *Int. J. Primatol.*, 16: 807–833.
- DORAN, D. 1992a. Comparison of instantaneous and locomotor bout sampling methods: a case study of adult male chimpanzee locomotor behavior and substrate use. *Amer. J. Phys. Anthropol.*, 89: 85–99.
- DORAN, D. 1992b. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study of paedomorphism and its behavioral correlates. *J. Human Evol.*, 23: 139–157.
- DORAN, D. 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. *Amer. J. Phys. Anthropol.*, 91: 99–116.
- DORAN, D.; HUNT, K. 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In: *Chimpanzee Cultures*, WRANGHAM, R.; MCGREW, W.; DE WAAL, F.; HELTNE, P. (eds.), Harvard Univ. Press, Cambridge, Massachusetts, pp. 93–108.
- EDGINGTON, E. 1987. *Randomization Tests*. Marcel Dekker, New York.
- FLEAGLE, J. G. 1976. Locomotion and posture of the Malayan Siamang and implications for Hominoid evolution. *Folia Primatol.*, 26: 247–269.
- FLEAGLE, J. G.; MITTERMEIER, R. A. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *Amer. J. Phys. Anthropol.*, 52: 301–314.
- GANZHORN, J. U. 1989. Niche separation of seven lemur species in the eastern rainforest of Madagascar. *Oecologia*, 79: 279–286.
- GARBER, P. A.; PREUTZ, J. D. 1995. Positional behavior in moustached tamarin monkeys: effects of habitat on locomotor variability and locomotor stability. *J. Human Evol.*, 28: 411–426.
- GAUTIER-HION, A.; GAUTIER, J. P.; QURIS, R. 1981. Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Terre et Vie*, 35: 511–536.
- GEBO, D. L. 1987. Locomotor diversity in prosimian primates. *Amer. J. Primatol.*, 13: 271–281.
- GEBO, D. L. 1992. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *Amer. J. Primatol.*, 26: 277–290.
- GEBO, D. L.; CHAPMAN, C. A. 1995a. Habitat, annual and seasonal effects on positional behavior in red colobus monkeys. *Amer. J. Phys. Anthropol.*, 96: 73–82.
- GEBO, D. L.; CHAPMAN, C. A. 1995b. Positional behavior in five sympatric Old World monkeys. *Amer. J. Phys. Anthropol.*, 97: 49–76.
- GENTRY, A. H. 1982. Patterns of neotropical plant species diversity. *Evol. Biol.*, 15: 1–84.
- GLANDER, K. E.; WRIGHT, P. C.; DANIELS, P. S.; MERENLENDER, A. 1992. Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *J. Human Evol.*, 22: 1–17.
- HARCOURT, C. S.; NASH, L. T. 1986. Species differences in substrate use and diet between sympatric galagos in two Kenyan coastal forests. *Primates*, 27: 41–52.
- MCGRAW, W. S. 1996. Cercopithecoid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. *Amer. J. Phys. Anthropol.*, 100: 507–522.
- MEDLEY, K. E. 1993. Primate conservation along the Tana River, Kenya: an examination of the forest habitat. *Cons. Biol.*, 7: 109–121.
- MENDEL, F. 1976. Postural and locomotor behavior of *Alouatta palliata* on various substrates. *Folia Primatol.*, 26: 36–53.
- MITTERMEIER, R. A. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatol.*, 30: 161–193.
- OVERDORFF, D. J. 1991. Ecological correlates to social structure in two prosimian primates: *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. Ph. D. thesis, Duke Univ., North Carolina.
- OVERDORFF, D. J. 1993. Ecological and reproductive correlates to range use in red-bellied lemurs (*Eulemur rubriventer*) and Rufous lemurs (*Eulemur fulvus rufus*). In: *Lemur Social Systems and Their Ecological Basis*, KAPPELER, P.; GANZHORN, J. (eds.), Plenum Press, New York, pp. 167–178.
- OVERDORFF, D. J. 1996. Ecological correlates to social structure in two lemur species in Madagascar. *Amer. J. Phys. Anthropol.*, 100: 487–506.
- RICHARD, A. 1978. *Behavioral Variation: Case Study of a Malagasy Lemur*. Bucknell Univ. Press, Lewisberg, Pennsylvania.

- RICHARD, A. 1979. Intraspecific variation in the social organization and ecology of *Propithecus verreauxi*. In: *Primate Ecology: Problem Oriented Field Studies*, SUSSMAN, R. (ed.), John Wiley & Sons, New York, pp. 23–51.
- RIPLEY, S. 1967. The leaping of langurs: a problem in the study of locomotor adaptation. *Amer. J. Phys. Anthropol.*, 26: 149–170.
- RIPLEY, S. 1977. Gray zones and gray langurs: Is the “semi-” concept seminal? *Yrbk. Phys. Anthropol.* 1976, 20: 376–394.
- RIPLEY, S. 1979. Environmental grain, niche diversification, and positional behavior in Neogene primates: an evolutionary hypothesis. In: *Environment, Behavior, and Morphology: Dynamic Interactions in Primates*, MORBECK, M.; PREUSCHOFF, H.; GOMBERG, N. (eds.), Gustav Fischer, New York, pp. 37–74.
- RODMAN, P. S. 1991. Structural differentiation of microhabitats of sympatric *Macaca fascicularis* and *M. nemestrina* in East Kalimantan, Indonesia. *Int. J. Primatol.*, 12: 357–375.
- SA, R. M. L.; STRIER, K. B. 1992. A preliminary comparison of forest structure and use by two isolated groups of woolly spider monkeys, *Brachyteles arachnoides*. *Biotropica*, 24: 455–459.
- STALLINGS, J. R.; WEST, L.; HAHN, W.; GAMARRA, I. 1989. Primates and their relation to habitat in the Paraguayan Chaco. In: *Advances in Neotropical Mammalogy*, REDFORD, K.; EISENBERG, J. (eds.), Sandhill Crane Press, Gainesville, pp. 425–441.
- STRIER, K. 1987. Ranging behavior of woolly spider monkeys or muriquis (*Brachyteles arachnoides*). *Int. J. Primatol.*, 8: 575–591.
- WHITE, F. J.; OVERDORFF, D. J.; BALKO, E. A.; WRIGHT, P. C. 1995. Distribution of ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. *Folia Primatol.*, 64: 124–131.
- WRIGHT, P. C. 1986. Ecological correlates to monogamy. In: *Primate Ecology and Conservation*, ELSE, J.; LEE, P. (eds.), Cambridge Univ. Press, Cambridge, pp. 159–168.
- WRIGHT, P. C. 1992. Primate ecology, rainforest conservation, and economic development: building a national park in Madagascar. *Evol. Anthropol.*, 1: 25–33.
- WRIGHT, P. C. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *Int. J. Primatol.*, 16: 835–854.
- WRIGHT, P. C. 1997. The future of biodiversity in Madagascar. In: *Natural Change and Human Impact in Madagascar*, GOODMAN, S. M.; PATTERSON, B. D. (eds.), Smithsonian Inst. Press, Washington, pp. 381–405.

— Received: November 15, 1996; Accepted: April 17, 1998

Authors' Names and Addresses: MARIAN DAGOSTO, *Department of CMS Biology, Northwestern University Medical School, 303, E. Chicago Avenue, Chicago, Illinois 60611-3008, U. S. A.* e-mail: m-dagosto@nwu.edu and *Research Associate, Department of Mammalogy, American Museum of Natural History, and Research Associate, Division of Zoology, Department of Mammals, Field Museum of Natural History*; NAYUTA YAMASHITA, *Department of Anatomy, University of Hong Kong, Li Shu Fan Building, 5 Sassoan Road, Hong Kong.*