Effects of Housing Differences Upon Activity Budgets in Captive Sifakas (*Propithecus verreauxi*)

Joseph M. Macedonia

Duke University, Department of Anthropology, Durham, North Carolina

Activity budgets of captive sifakas (*Propithecus verreauxi coquereli* and *Propithecus verreauxi verreauxi*) were assessed from 500 hours of observational data obtained at the Duke University Primate Center (Durham, NC). Data were examined for behavioral differences according to gender, availability of intergroup contact, subspecies, indoor/outdoor housing, and enclosure size. Results showed few differences between the activity budgets of males and females. Several differences found in conjunction with availability of intergroup contact appeared to relate more to subspecific, than to contact, differences. Sifakas housed outdoors were more active, spending less time resting and more time in locomotion, feeding, and playing than sifakas housed indoors. The findings of this study implicate outdoor housing as a primary factor in stimulating activity in these rare prosimian primates.

INTRODUCTION

Lemurs of the family Indriidae are exceedingly difficult to maintain in a captive setting due, in part, to their specialized folivorous diet. Only one indriid species, Verreaux's sifaka (*Propithecus verreauxi*), has ever been sustained in captivity in the U.S. All sifakas presently living outside Madagascar are part of a breeding colony at the Duke University Primate Center (DUPC) in Durham, North Carolina. In the wild, *P. verreauxi* live in what have been termed "foraging groups." These groups vary widely in size (range = 2 to 12 individuals) and in adult sex ratio (females per male: 0.25 to 5.0), although population-wide sex ratios appear to approach unity [Richard, 1978a, 1985]. The DUPC has housed sifakas in pairs and trios since 1968, but only a single captive-born individual has survived to adulthood and produced offspring.

In an effort to improve the general health and breeding success of these captive prosimians, changes in their diet (increased quantity and variety of browse) and environment (limited intergroup contact and outdoor housing) were instituted. The present study examines the effects of housing differences upon activity budgets in experimental and control groups of *P. verreauxi*. When possible, results of this study are compared to data from wild sifakas.

METHODS
Subjects and Housing
The five groups observed in this study were comprised of 11 sifakas of two subspecies; seven Coquerel's sifakas (*Propithecus verreauxi coquereli*—four males, three females) and four Major's sifakas (*P. v. verreauxi*, form: *majori*—two males, two females). Morphological descriptions and distributions for these two subspecies can be found in Tattersall [1982]. Biographical, housing, and group configuration data are presented in Table 1. All but one of the animals were wild-caught. Age estimations for wild-caught animals were based on evaluation of dentition at time of capture.

During phase 1 of three study phases, all groups were housed indoors in hexagonal enclosures with an approximate volume of 82 m³ [Klopfer and Boskoff, 1979]. A general description of enclosure furnishings can be found elsewhere [Bergeron, 1974; Eaglen and Boskoff, 1978; Klopfer and Boskoff, 1979]. No windows or skylights were present in the indoor enclosures. The light/dark cycle was synchronized with North Carolina time and controlled by automatic timers coupled to the incandescent and fluorescent enclosure lighting. The indoor rooms were maintained at approximately 76°F year-round.

Group differences in housing were as follows. Four of the five study groups (groups 1, 2, 4, and 5) were adult male/female pairs; group 3 contained an adult pair and a subadult male. Group 5 (phases 1 and 2) and group 4 (phase 3) were the only

TABLE 1. *Propithecus verreauxi* study groups

Group No.	Name	Sex	Sub- species	Date of birth	Housing condition	Phase 1[a]	Phase 2	Phase 3
1	Nigel[b]	M	Pvc[c]	2/10/77	Isolated	Indoor	Indoor	N/A
1	Livia	F	Pvc	≈1979	pair			
2	Augustus	M	Pvc	≈1978	Isolated	Indoor	Indoor	N/A
2	Julia	F	Pvc	≈1977	pair			
3	Trajan	M	Pvc	≈1980	Isolated	Indoor	Outdoor	N/A
3	Hadrian	M	Pvc	≈1982	trio			
3	Cornelia	F	Pvc	≈1977				
4	Caesar	M	Pvv[d]	≈1980	Contact	Indoor	Indoor	Indoor/
4	Calpurnia	F	Pvv	≈1979	pair			outdoor
5	Justinian	M	Pvv	≈1980	Contact	Indoor	Indoor	N/A
5	Theodora	F	Pvv	≈1981	pair			

[a]Phase 1, February–March, 1985; phase 2, June–August, 1985; Phase 3, August, 1986.
[b]Captive-born at DUPC; all others wild-caught.
[c]*Propithecus verreauxi coquereli*.
[d]*Propithecus verreauxi verreauxi* (form: *majori*).

sifaka groups housed with another uncaged lemur species: a mated pair of gray gentle lemurs (*Hapalemur griseus griseus*). Unlike the caged mated pair of Coquerel's mouse lemurs (*Mirza coquereli*) present in all the indoor sifaka enclosures, the *Hapalemur* moved freely throughout the environment. Despite occasional aggressive interactions (in the form of lunges and retreats), the prevailing attitude between *Propithecus* and *Hapalemur* was one of indifference. During phases 1 and 2, the two adjacent rooms which contained the two pairs of *P. v. verreauxi* (groups 4 and 5) allowed visual, auditory, olfactory, and limited tactile contact through a wire grid "window" (approximately 0.5 m^2). Group 3 was relocated into an outdoor enclosure for phase 2. This enclosure (approximately 234 m^3) measured nearly three times the volume of the indoor hexagonal rooms and included more supports that could be used in locomotion. Bamboo grew in this outdoor enclosure and provided some shade. This bamboo was sometimes used for support during locomotion and play, but was never observed to be ingested by the sifakas. Observations of group 3 in this enclosure were begun after an acclimation period of 10 days. A smaller outdoor enclosure (approximately 60 m^3) was made available to group 4 during phase 3. This outdoor annex was directly accessible from the indoor room and allowed unobstructed movement between the two environments. Furnishings in this enclosure were similar to those of the indoor rooms. The total combined volume of the indoor and outdoor compartments was approximately 142 m^3. Observations of group 4 were begun approximately 10 weeks after outdoor housing was first made available to this group.

Food

During phase 1, the animals were fed mixed fruits, vegetables, and commercial monkey chow once daily. A variety of additional items such as cottage cheese and hard boiled eggs were usually provided, and vitamin supplements were added to the water supply. Mango leaves, shipped from Florida, were also offered daily. During phases 2 and 3, the sifakas' diet was heavily supplemented with fresh local foliage such as sweet gum, mimosa, hornbeam, red bud, sumac, blackberry, and wild rose.

Procedure

Observational data were gathered during the months of February and March, 1985 (phase 1), June–August, 1985 (phase 2), and August, 1986 (phase 3). During phase 1, 2 hours of data collection were conducted during each 1-hour period between 07:00–17:00 hours, inclusive. This resulted in 22 hours of observation per group. During phase 2 (1985) and phase 3 (1986), 5 hours of data collection were conducted during each 1-hour period between 07:00–19:00 hours, inclusive. This resulted in 65 hours of observation per group. Total observation hours were as follows: phase 1–110 hours; phase 2–325 hours; phase 3–65 hours.

Data were collected (see Table 2) at 5-minute intervals using the scan sampling technique [Altmann, 1974]. Each datum obtained in this way represents one "individual activity record" (IAR). Data were gathered in hour-long increments, and observation sessions generally lasted from 2 to 5 hours. Ambient temperature and degree of cloud cover (on a three-point qualitative scale) were recorded at the half-hour mark of each hour-long sample. Data collection on outdoor groups continued during light, intermittent rain showers but was terminated at the onset of heavy rainfall.

Statistical Analyses

All tests performed were nonparametric, two-tailed, and P-values were corrected for ties. These tests included the Mann-Whitney U Test, the Wilcoxon Matched-

TABLE 2. Behavioral definitions

Behavior	Definition
Resting	A motionless state with eyes open or closed
Scanning[a]	Visual exploration of the environment
Comfort movement[a]	Shifting body position, stretching, scratching
Hanging[a]	Motionless suspension from a substrate
Inactivity	An artificial category partitioning "inactive" behaviors (above) from "active" behaviors (below)
Locomotion	Vertical clinging and leaping, bipedal hopping or walking, quadrupedal walking, climbing, brachiating
Feeding	Ingestion of food or water
Autogrooming	Use of the tooth comb, tongue, or grooming claw to remove debris and/or parasites from the body
Allogrooming	Grooming of a group-mate as described above
Playing	Rope-swinging, rapid ricocheting (alone or in a "game of tag"), wrestling
Aggression	Lunges, cuffs, or bites directed at a group-mate
Scent-marking	Throat-marking (males), anogenital (incl. urine) marking, endorsing (male overmarking of female marks)

[a]Behaviors not subjected individually to statistical testing.

Pairs Signed-Ranks Test, the Kolmogorov-Smirnov Two-Sample Test, and Spearman Rank Correlation. Only totals of IARs or IARs per hour were used for testing purposes.

RESULTS

A comparison of behavioral frequencies as percentages of total activity is presented for males and females in Figure 1. The data (pooled across phases 1 and 2) revealed one sexually diethic difference: female sifakas (n = 5) groomed their male group-mates (n = 6) significantly less often than they were groomed by those same males (U = 0; P < .01).

Of the four groups housed indoors during phases 1 and 2 (Table 1; Fig. 2), the two groups without intergroup contact (groups 1 and 2–*P. v. coquereli*; n = 4) both fed (U = 1; P < .05) and played (U = 1; P < .05) significantly more often than the two groups provided with limited intergroup contact (groups 4 and 5–*P. v. verreauxi*; n = 4). These two variables (feeding and playing) were positively correlated (P ≤ .05; Table 3).

Changes in activity patterns of group 3 (*P. v. coquereli*) associated with being moved from an indoor room to a larger outdoor enclosure were investigated in several ways. First, data from phase 1 were examined to see if group 3 differed in frequency of behaviors from the other four groups *before* being moved to their outdoor habitat. While slight differences in activity budgets were apparent (Fig. 3a), none were statistically significant.

Second, data from phase 2 were compared between the outdoor and indoor groups to examine differences in activity budgets potentially attributable to different housing environments (Fig. 3b). Results showed that members of the group housed outdoors (group 3; n = 3) rested significantly less often (U = 1.5; P < .05), were inactive significantly less often (U = 0; P < .05), and were observed in locomotion (U = 2; P < .05), feeding (U = 0; P < .05), and playing (U = 2; P < .05)
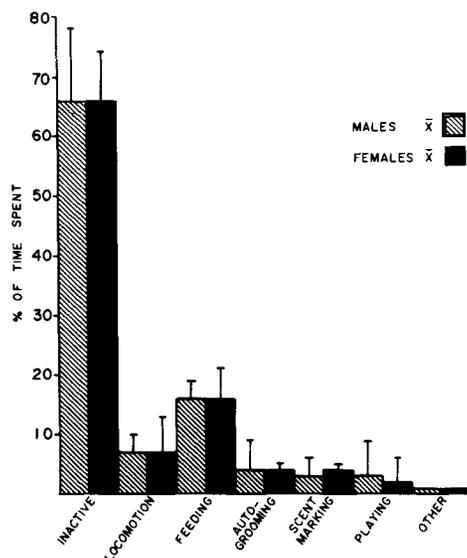
Fig. 1. Comparison of activity budgets between males and females as a percentage of total activity. Top of bracket = 1 SD.
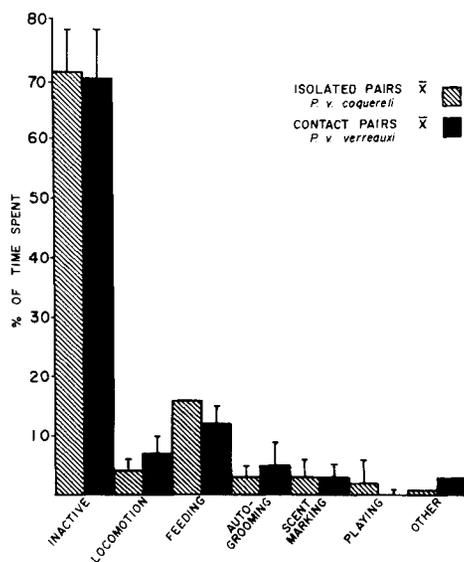

Fig. 2. Comparison of activity budgets between sifaka subspecies as a percentage of total activity for groups 1, 2, 4, and 5. SD for FEEDING (hatched) less than 1%.

significantly more often than members of the groups housed indoors (groups 1, 2, 4, and 5; n = 8).

Third, activity budgets within groups were examined by comparing phases 1 and 2. Sample size was too small for such a comparison in group 3 (n = 3 group members, or "cases"), but activity level increases in this group accompanying the move outdoors were evident (Fig. 4). Results for the four indoor groups (n=8)

TABLE 3. Correlation among behavioral categories*

	Resting	Inactivity	Locomotion	Feeding	Autogrooming	Allogrooming	Scent-marking	Playing
Inactivity	+[a]							
Locomotion	−	−						
Feeding	(−)	(−)	NS					
Autogrooming	NS	NS	NS	NS				
Allogrooming	NS	NS	NS	NS	NS			
Scent-marking	NS	NS	NS	NS	NS	NS		
Playing	NS	NS	NS	(+)	(−)	NS	NS	
Aggression	NS	NS	(+)	NS	NS	NS	NS	NS

*Correlations are IAR totals pooled for study phases 1 and 2.

[a] +, Positive correlations, −, negative correlations. Symbols in parentheses; $P \leqslant .05$; all other symbols, $P \leqslant .01$, NS, not significant.
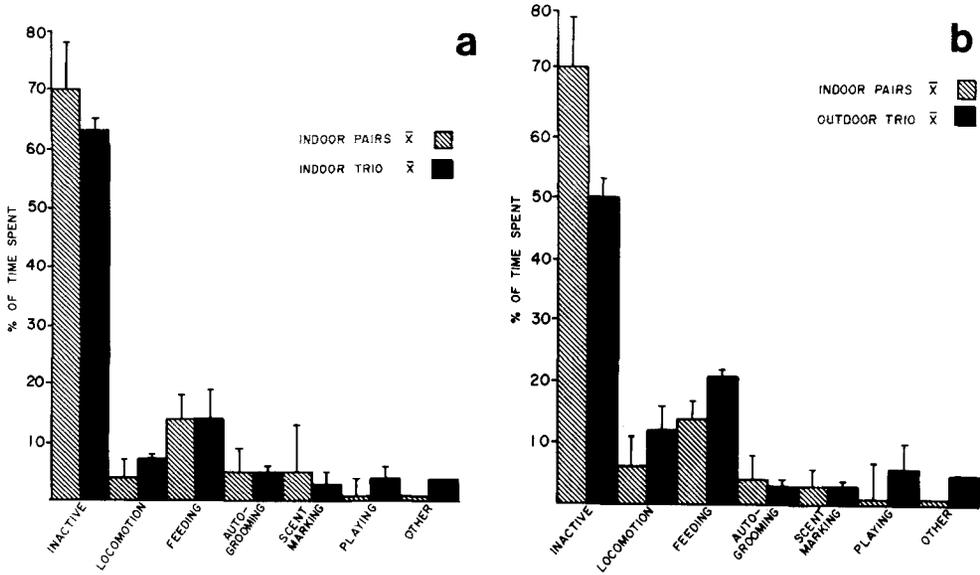
Fig. 3a. Comparison of activity budgets between indoor pairs (groups 1, 2, 4, and 5) and the trio (group 3) during phase 1.

Fig. 3b. Comparison of activity budgets between indoor pairs (groups 1, 2, 4, and 5) and the trio (group 3) during phase 2.
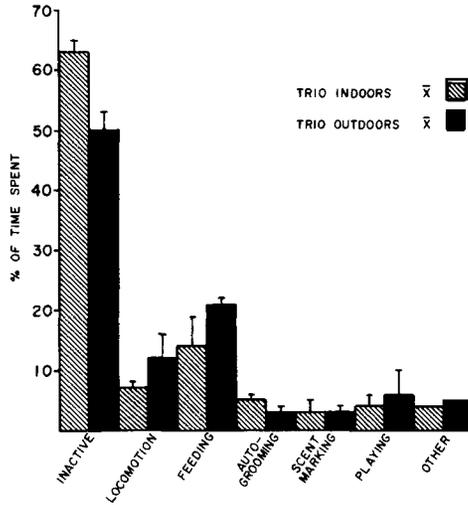

Fig. 4. Comparison between indoor (phase 1) and outdoor (phase 2) activity budgets for the trio (group 3).

revealed a significant increase in time spent resting (W = 2.10; P < .05) and allogrooming (W = 1.96; P < .05) in phase 2 over phase 1. These two variables were not significantly correlated with one another (Table 3).

Temporal distributions of behaviors were investigated to discover if different housing environments might have influenced patterns of activity across the daily diurnal cycle. No significant differences existed in conjunction with gender, although females were slightly more active than males during most hours of the day (Fig. 5).
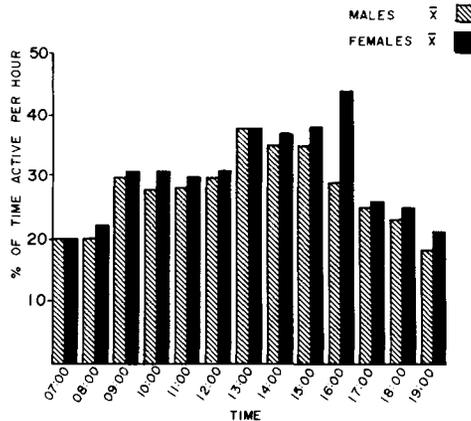
Fig. 5. Comparison of temporal distributions of activity for males and females (phase 2).

Although not significant, strong subspecific differences in the location of peak activity periods between the indoor groups can be seen (Fig. 6). Mid-morning and early-afternoon peaks occur for *P. v. coquereli*, whereas a slow building of activity toward a late-afternoon/early-evening peak is found for *P. v. verreauxi*. Temporal differences in frequency of activity were significant, however, in the comparisons between group 3 (n = 3) and: a) the indoor groups without intergroup contact (n = 4; D = 1.96; P < .001); b) the indoor groups with intergroup contact (n = 4; D = 1.96; P < .001); and c) the pooled data from all indoor groups (n = 8; D = 2.35; P < .001; Fig. 7).

Because of increased activity levels associated with the relocation of group 3 from an indoor to an outdoor enclosure (phase 2), correlations were calculated between the number of IARs spent inactive during each hour of observation and the variables of ambient temperature (mean = 78.8°F; SD = 5.6°F), degree of cloud cover, and time of day. Results showed no significant correlations between frequency of activity and any of these variables.

Data obtained for group 4 (*P. v. verreauxi*) during phase 3 were also examined for effects of access to an outdoor enclosure. Because the same number of observation hours for this group was obtained in both phase 2 and phase 3 (65 hours each), pairwise comparisons could be made directly between the two study phases. Data were paired by hour of the day (n = 13) for each behavioral category.

Results for group 4 revealed significant decreases in inactivity (W = 3.01; P < .005) and resting (W = 2.97; P < .005), and significant increases in locomotion (W = 3.18; P < .005) and playing (W = 2.20; P < .05) in phase 3 over phase 2 (Fig. 8). Increases in time spent feeding also were apparent and approached significance (W = 1.64; P = .1). In addition, temporal distributions of activity in group 4 were significantly different between the two study phases (D = 1.77; P < .005; Fig. 9).

Because the indoor and outdoor compartments housing group 4 during phase 3 differed in volume, the relative importance of housing environment and enclosure size could be investigated. Results showed that group 4 spent only 7.8% (122 of 1,560 IARs) of its time in the larger indoor compartment, whereas the remaining 92.2% (1,438 IARs) of the phase 3 activity budget was spent in the smaller outdoor
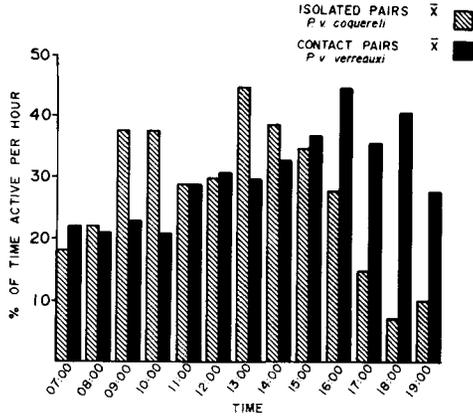
Fig. 6. Comparison of temporal distributions of activity for both sifaka subspecies (phase 2).
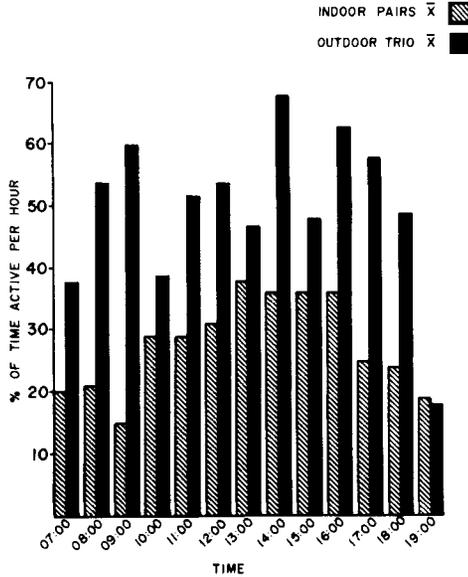

Fig. 7. Comparison of temporal distributions of activity for the indoor pairs (groups 1, 2, 4, and 5) and the outdoor trio (group 3) during phase 2.

compartment. Moreover, well over half of the time spent indoors (62.3%; 76 IARs) was exclusive to feeding. Because food trays and foliage-on-the-branch were placed in the indoor *and* outdoor compartments, group members would forage indoors on occasion when the selection of food items outdoors was (apparently) unsatisfactory. A further proportion of the time (14.8%; 18 IARs) spent in the relatively warm (76°F) indoor room was related directly to thermoregulation. On two consecutively cool mornings (54–56°F), several bouts of inactivity were recorded as the two group members sat in close proximity to indoor heat lamps. Taken together, foraging and thermoregulation accounted for over three-fourths (77%) of the time spent indoors.
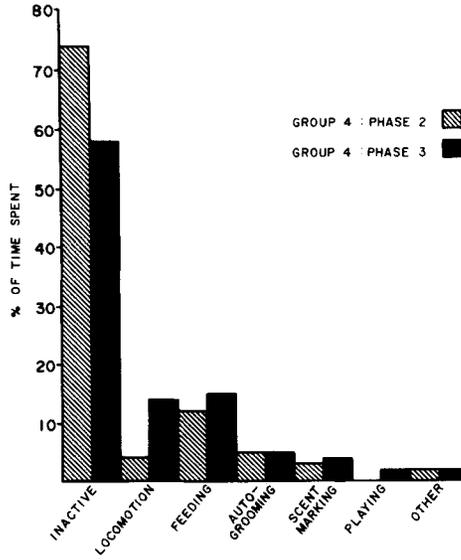
Fig. 8.   Comparison between indoor (phase 2) and outdoor (phase 3) activity budgets for group 4.
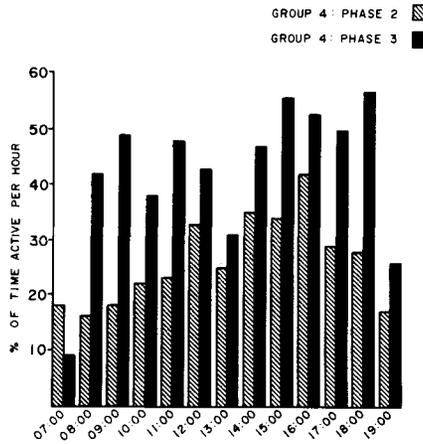

Fig. 9.   Comparison of temporal distributions of activity in group 4. Phase 2: indoor housing; phase 3: indoor/outdoor housing.

Correlations were calculated between time spent inactive by group 4 in phase 3 and ambient temperature (mean = 75.0°F; SD = 7.8°F), degree of cloud cover, and time of day. Results showed time of day to be the only variable correlated with inactivity (n = 65 hours; r_s = $-$.2621; P < .05).

DISCUSSION

The analyses described above compared frequency of behaviors in terms of one of three grouping criteria: 1) gender; 2) availability of intergroup contact/subspecies; or 3) housing location/enclosure size. Only one gender-related behavioral difference was found: males groomed females on more occasions than the reverse behavior

occurred. This gender difference in allogrooming frequency also was seen as a trend in wild sifakas [Richard, 1974, 1978a; Richard & Heimbuch, 1975].

The more frequent observations of feeding and playing among the indoor *P. v. coquereli* groups over the *P. v. verreauxi* groups might be better interpreted in terms of subspecific behavioral variation than availability of intergroup contact. In Madagascar, Richard [1974, 1977, 1978a,b] found that during the wet season, when food resources were most plentiful for both subspecies, *P. v. coquereli* did not differ significantly from *P. v. verreauxi* in the amount of time devoted to foraging. In the dry season, however, the southern *P. v. verreauxi* fed significantly less often than the northern *P. v. coquereli*. This change associated with the dry season appeared to be attributed to a greater reduction in food availability and diversity in the south at this time of year. In an energetic context, the *P. v. verreauxi* may have reduced their foraging efforts as a result of the less rewarding harvest of food resources during the dry season. The findings of the present study could indicate that an analogous decrease in quantity and diversity of food items associated with the change from a natural to a captive diet may be at least partially responsible for the lower feeding frequency of *P. v. verreauxi* (as compared to *P. v. coquereli*) at the DUPC.

A corollary of this apparent energy budget depression relates to the lower frequency of play behavior seen in *P. v. verreauxi* (as compared to *P. v. coquereli*) in Madagascar. The likelihood of energetic stress imposed upon both subspecies during the dry season (due to decreased harvesting efficiency and also thermoregulatory stress associated with seasonally colder ambient temperatures) may be, as mentioned above, more extreme for *P. v. verreauxi* in the south; but the harsh, arid southern habitat may actually cause the southern species to live closer to its energy budget limits even during the wet season. Richard's [1978a] data show that as a possible reflection of energy conservation, all playing behavior ceased in both subspecies during the dry season. These data also show, however, that during the wet season when playing was observed, *P. v. verreauxi* still played only about 34% as much as did *P. v. coquereli*. Thus, the significantly lower frequencies of feeding and playing exhibited by *P. v. verreauxi* in captivity may represent retentions of naturally adaptive behaviors observed in the wild.

The most notable behavioral differences which relate to the captive management of sifakas are apparent in the comparisons of the indoor vs outdoor housing conditions. No significant differences in behavior existed between group 3 and the other four groups during phase 1 of the study. Moreover, the negative correlations of feeding and locomotion with inactivity and resting (Table 3) suggest that time spent in the former two behaviors was replacing that spent in the latter by group 3 in the out-of-doors. This would imply that: a) increases in activity frequencies of group 3 can be accounted for by the move from an indoor to an outdoor environment, and b) group size (at least as pairs vs trios) may not represent a confounding variable affecting the frequency of activity in captive sifakas. Nevertheless, because this trio was also slightly more active than other groups when housed indoors (Fig. 3a), the present results must be interpreted cautiously. Note, however, that the significantly greater frequency of time spent feeding for group 3 over the indoor groups in phase 2 (Fig. 3b) showed no such tendencies during phase 1 (Fig. 3a). Furthermore, despite the copious provisions of foliage received by the indoor groups during Phase 2, *their* feeding frequencies did not increase over phase 1 when they were receiving relatively small amounts of foliage.

Comparable results were found for group 4 in phase 3. When given access to the out-of-doors, activity increases were seen in locomotion, feeding, and playing. It

seems noteworthy that these increases (Fig. 8) still conform to the subspecific pattern of activity budget differences found in phase 2. That is, when housed in similar environments, *P. v. verreauxi* appear to feed and play less often than *P. v. coquereli.*

Apart from the overall activity increases of group 4 in phase 3, significant differences in the temporal distribution of activity also were seen. These differences occurred primarily between the hours of 08:00 and 12:00. The slow building of activity across these hours during phase 2 was replaced in phase 3 by an oscillating pattern of relatively high activity levels (Fig. 9). Notably, this phase 3 activity pattern for *P. v. verreauxi* resembles that of the outdoor-housed *P. v. coquereli* in phase 2 (Fig. 7). Although relative activity peaks differed slightly in the two subspecies when housed outdoors, the overall temporal distributions of activity were more similar than different. This finding agrees reasonably well with data obtained for sifakas in the wild [Richard, 1978a]. Given that photophase was the same for both captive subspecies, the temporal differences in activity patterns of the indoor groups remain unexplained.

Subspecific comparisons of activity budgets aside, the most important and useful finding in this study is that levels of activity can be increased most dramatically in sifakas by providing them with an outdoor living space. As clearly borne out in the results of phase 3, when given a choice between indoor and outdoor housing, sifakas *choose* to be outside.

CONCLUSIONS

1. Male sifakas groomed their female group-mates significantly more often than the reverse behavior occurred. No other activities differed significantly in frequency between the sexes.

2. Significant differences in the frequencies of feeding and playing, along with differences in the temporal distribution of activity, appeared to relate more to subspecific variation than to availability of intergroup contact.

3. Relocation (group 3) or access to (group 4) an outdoor environment significantly diminished inactivity and stimulated locomotion, feeding, and playing in two groups of sifakas. Although group size and enclosure size may be pertinent, the results of this study suggest outdoor housing as the primary factor augmenting activity levels in captive sifakas.

ACKNOWLEDGMENTS

REFERENCES

Altmann, J. Observational study of behavior: Sampling methods. BEHAVIOUR 49:227–265, 1974.
Bergeron, J.A. A prosimian research colony, pp 201–211 in PROSIMIAN BIOLOGY. R.D. Martin; G.A. Doyle; A.C. Walker, eds. London, Duckworth, 1974.
Eaglen, R.H.; Boskoff, K.J. The birth and early development of a captive sifaka, *Propithecus verreauxi coquereli.* FOLIA PRIMATOLOGICA 30:206–219, 1978.

Klopfer, P.H.; Boskoff, K.J. Maternal behavior in prosimians, pp 123–156 in THE STUDY OF PROSIMIAN BEHAVIOR. G.A. Doyle; R.D. Martin, eds. New York, Academic Press, 1979.

Richard, A.F. Intra-specific variation in the social organization and ecology of *Propithecus verreauxi*. FOLIA PRIMATOLOGICA 22:178–207, 1974.

Richard, A.F. The feeding behavior of *Propithecus verreauxi*, pp 71–96 in PRIMATE ECOLOGY: STUDIES OF FEEDING AND RANGING BEHAVIOR IN LEMURS, MONKEYS, AND APES. T. Clutton-Brock, ed. New York, Academic Press, 1977.

Richard, A.F. BEHAVIORAL VARIATION: CASE STUDY OF A MALAGASY LEMUR. Lewisburgh, Bucknell University Press, 1978a.

Richard, A.F. Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi:* Lemuriformes, pp 519–534 in THE ECOLOGY OF ARBOREAL FOLIVORES. G.G. Montgomery, ed. Washington, D.C., Smithsonian Institution Press, 1978b.

Richard, A.F. Social boundaries in a Malagasy prosimian, the sifaka (*Propithecus verreauxi*). INTERNATIONAL JOURNAL OF PRIMATOLOGY 6:553–568, 1985.

Richard, A.F.; Heimbuch, R. An analysis of the social behavior of three groups of *Propithecus verreauxi*, pp 313–333 in LEMUR BIOLOGY. I. Tattersall; R.W. Sussman, eds. New York, Plenum Press, 1975.

Tattersall, I. THE PRIMATES OF MADAGASCAR. New York, Columbia University Press, 1982.