Zoo Biology 13:333–344 (1994)

Locomotion of Free-Ranging Golden Lion Tamarins (*Leontopithecus rosalia*) at the National Zoological Park

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Locomotor behavior and substrate use of cage-reared golden lion tamarins (*Leontopithecus rosalia*), newly released and free-ranging on the grounds of the National Zoological Park, were studied to determine if locomotion changed following exposure to naturalistic conditions. The animals employed a predominantly quadrupedal locomotor profile, incorporating leaping and vertical climbing to a lesser degree. There was no clear evidence of a change in locomotion due to the high degree of variability in these behaviors. The locomotor repertoire of the free-ranging group differed from that of groups occupying unenriched but relatively large conventional enclosures, indicating that whereas locomotion is plastic with respect to environment, substrate characteristics influence locomotor behavior and may promote stereotypical behavior. However, due to anatomical constraints, the locomotor repertoire tended to be less variable than substrate use. Similar behaviors were used in moving through a variety of habitat features in spite of strong associations between specific locomotor styles and substrate classes.

Key words: New World monkeys, Platyrrhini, Callitrichinae, stereotypy, video, reintroduction

INTRODUCTION

The effect of environment on the positional behavior, posture and locomotion [Prost, 1965] of arboreal mammals is not well known. Although there is a growing literature on the locomotor behavior of wild neotropical primates [e.g., Kinzey, 1977; Fleagle, 1988; Garber, 1992; Gebo, 1992], little is known about intraspecific (or intrageneric) locomotor variability in relation to habitat differences. Even less is

Received for publication February 3, 1993; revision accepted April 3, 1994.

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known about gross environmental effects such as those found in captivity. There is, however, a widespread presumption that captivity may influence skeletal form; researchers often exclude the bones of zoo animals from their statistical samples. Information on these effects is important to morphologists concerned with form and function, to paleontologists concerned with inferring the behavior of extinct animals, to conservationists interested in the reintroduction of endangered species to the wild, and to a broad range of specialists concerned with the physical and psychological well-being of captive animals [e.g., Bayne, 1991; Beck et al., 1991; Line, 1987; Chamove, 1989; Chamove and Rohrhuber, 1989; Line et al., 1989].

Thus as zoological parks seek to elicit "wild" behavior by exhibiting primates and other mammals in more naturalistic settings, there is a unique opportunity and a pragmatic need to examine the consequences of arboreal exposure. For example, Price [1992] investigated the locomotor proficiency and substrate preference of a cage-reared group of cotton-top tamarins (*Saguinus oedipus*) released into a wood at the Jersey Wildlife Preservation Trust and found changes in locomotor behavior over time.

Here, we report on a group of *Leontopithecus rosalia* released into Beaver Valley, a patch of forest at the National Zoological Park in Washington, DC. This study evaluates the effects of exposure to a naturalistic environment on the locomotor behavior of cage-reared animals and emphasizes the relationships between various locomotor styles and substrate classes in captive populations.

Given that *L. rosalia* have been perceived to manifest a locomotor deficit upon reintroduction to the wild [Kleiman et al., 1986; Beck et al., 1994], we were interested in the response of locomotor behavior to exposure to a naturalistic setting. The effect of substrate availability on the locomotor profile was investigated, and the locomotor behavior of the Beaver Valley group was compared to a second group housed in more conventional enclosures.

L. rosalia were first released in the National Zoological Park in 1986 to develop and test postrelease training as a reintroduction technique [Bronikowski et al. 1989]. Postrelease training, which has improved the success and cost-effectiveness of reintroduction [Beck et al., 1991, 1994], is predicated on the assumption that newly released tamarins provided with food, shelter, and a stable social group will gradually expand their range, thus increasing their opportunities to learn to find food, locomote on natural substrates, and orient in novel surroundings. The free-ranging exhibit has stimulated research, reinforced public conservation education programs, and become a regular summer feature at the National Zoo. This study was part of a larger project designed to compare locomotor behavior of captive and wild *L. rosalia,* to identify differences between captive-born and wild-born locomotor patterns, to assess possible environmental correlates of any differences, and to evaluate management strategies in relation to locomotion.

MATERIALS AND METHODS

Beaver Valley consists of ~0.2 hectares of forested hillside within the zoo. It provides the animals an opportunity for arboreal locomotion on a wide range of substrate types and sizes. The trees are mature beech and oak, forming an essentially continuous summer canopy, and an understory (< 3 m) of bushes and shrubs. To simulate a stratum utilized by wild *L. rosalia,* a hexagonal network of hemp ropes

(2.5 cm in diameter) was strung around the perimeter of the valley between tree trunks at a height of 3–7 m, passing through the understory at many points. An additional system of radial ropes connected a centrally located nest box to the points of the hexagon. The ropes could be raised or lowered on halyards. Midway through the study, on August 14, two of the 12 ropes were removed to determine whether the animals would use natural arboreal routes. Since the animals proved capable of negotiating these paths that the ropes circumvented, the ropes were not reinstalled. Bronikowski et al. [1989] provided details on daily management.

Subjects were a group of five *L. rosalia,* four males and one female, all identifiable by individual tail marks. One male, age 18, was the father of the other four, who were between 4 and 6 years old. Data were collected on 25 days between June 24 and October 12, 1991, beginning 4 days after the animals were released. Sampling days and observation periods were rotated to provide coverage of entire daily activities for every day of the week. Six data days were excluded from this analysis, as we required a minimum of 100 locomotor bouts per observation period for inclusion in the study, since samples of < 100 bouts tend to overrepresent single locomotor categories. Inter-observer error was determined to be < 5% by testing observers on the same video tape. Results are based on 4,566 locomotor bouts (Table 1) collected on 19 days and totaling 50 hr of observation.

The observational unit was a locomotor sequence, with each sequence composed of one or more locomotor bouts. A locomotor bout was defined [e.g., Fleagle and Mittermeier, 1980; Gebo, 1987] with reference to four concurrent elements:

(1) a discrete, uninterrupted movement displacing the center of gravity one or more body lengths; (2) maintenance of a definable locomotor pattern, such as walking or leaping; (3) use of only one class of support (as defined in Table 4); and (4) absence of postural interruptions lasting more than ~3 sec. Thus the series walk-leap-walk would be scored as three bouts within one sequence, and transitions from a thin to a thick branch using walking would represent two bouts of quadrupedalism. The use of one locomotor category across two substrates of the same class would represent one locomotor bout on one substrate class, as no functional change would be required of the animal. The end of a sequence was determined by the absence of movement for > 5 sec. Locomotion on the nest box and feeder was not scored as these movements rarely exceeded one body length.

Observational and video sampling (using a Hi-8 camcorder with telephoto lens) were used to collect sequence, bout, and substrate data. An individual's locomotion and substrate use were scored from the beginning to the end of a locomotor sequence. The location and behavior of most individuals could be continuously and simultaneously monitored, due to the size and character of the environment. As a result, it was possible to record locomotor sequences in their entirety.

Four of the five individuals were equally represented in our data set. They comprised 24%, 26%, 22%, and 22% of the sequences in which the identity of the animal could be determined (Table 2). The 18-yr-old male, by far the least active member of the group, contributed only 6% to the data set.

Although it is possible that ad libitum sampling may overrepresent dynamic or noisy behaviors, we feel that this was unlikely to be the case. All areas of the habitat were visible and golden lion tamarins are a strikingly colored, ostentatious species. We also determined that the number of bouts per sequence scored while the animals used the ropes (the most visible area of the habitat) was similar to the number of bouts

TABLE 1. Locomotion and substrate use in Beaver Valley

		Locomotion[a]						
Date	#Bouts	AQW	AQB	AQCb	L	BL	VCb	Su
27-Jun-91	279	44%	16%	5%	8%	9%	13%	2%
28-Jun-91	355	31%	23%	2%	13%	9%	20%	1%
11-Jul-91	234	31%	14%	7%	23%	3%	21%	1%
16-Jul-91	394	36%	11%	7%	15%	2%	24%	3%
18-Jul-91	233	36%	12%	13%	18%	1%	19%	0%
23-Jul-91	137	39%	11%	12%	13%	6%	12%	1%
24-Jul-91	318	34%	8%	15%	16%	3%	18%	3%
7-Aug-91	238	27%	18%	6%	15%	8%	23%	3%
8-Aug-91	252	40%	11%	8%	12%	3%	18%	5%
14-Aug-91	137	39%	17%	11%	12%	2%	15%	2%
14-Sep-91	359	34%	8%	12%	18%	8%	11%	2%
20-Sep-91	181	31%	12%	10%	17%	12%	12%	3%
24-Sep-91	122	29%	11%	14%	23%	6%	9%	3%
26-Sep-91	119	22%	8%	24%	29%	3%	5%	5%
4-Oct-91	102	28%	8%	18%	18%	7%	9%	10%
7-Oct-91	188	23%	10%	17%	32%	2%	11%	1%
8-Oct-91	496	23%	10%	23%	22%	2%	13%	3%
9-Oct-91	303	30%	13%	17%	20%	3%	10%	3%
12-Oct-91	119	29%	10%	14%	21%	8%	13%	2%
Total	4566	32%	12%	12%	18%	5%	15%	3%
St Dev	110	6%	4%	6%	6%	3%	8%	2%
CV	46	19	32	48	33	64	34	81

		Substrate[b]						
Date	# Bouts	#1	#1a	#2	#3	#4	Rope	#5
27-Jun-91	279	11%	3%	1%	6%	17%	57%	5%
28-Jun-91	355	19%	4%	3%	7%	13%	52%	2%
11-Jul-91	234	8%	2%	8%	0%	28%	34%	10%
16-Jul-91	394	6%	10%	5%	0%	22%	28%	24%
18-Jul-91	233	5%	10%	4%	0%	24%	28%	25%
23-Jul-91	137	5%	5%	2%	12%	24%	36%	8%
24-Jul-91	318	7%	3%	4%	9%	32%	29%	16%
7-Aug-91	238	18%	6%	5%	6%	9%	36%	16%
8-Aug-91	252	10%	4%	4%	8%	21%	29%	24%
14-Aug-91	137	8%	8%	0%	5%	18%	36%	23%
14-Sep-91	359	1%	4%	5%	15%	38%	14%	21%
20-Sep-91	181	3%	1%	4%	25%	27%	23%	16%
24-Sep-91	122	7%	11%	2%	15%	15%	28%	23%
26-Sep-91	119	3%	6%	4%	2%	23%	19%	43%
4-Oct-91	102	3%	3%	2%	13%	35%	29%	16%
7-Oct-91	188	9%	7%	1%	19%	16%	22%	26%
8-Oct-91	496	7%	9%	2%	12%	7%	23%	39%
9-Oct-91	303	5%	9%	2%	14%	18%	23%	30%
12-Oct-91	119	3%	3%	3%	3%	35%	30%	22%
Total	4566	8%	6%	3%	9%	21%	31%	21%
St Dev	110	5%	3%	2%	7%	8%	11%	10%
CV	46	65	55	62	76	40	34	50

[a] AQW, arboreal quadrupedal walking; AQB, arboreal quadrupedal bounding; AQCb, arboreal quadrumanous climbing; L, leaping; BL, bounding leaping; VCb, vertical climbing; Su, suspension.

[b] 1, vertical trunks, greater than armspan in diameter; 1a, vertical trunks, armspan in diameter; 2, boughs armspan in diameter; 3, branches, shoulder width, Ro, rope; 4, branches, hand width; 5, terminals (see text for further descriptions).

TABLE 2. Individual representation*

Individual[a]	Video	Visual	Total
82	7%	5%	6%
1,494	24%	25%	24%
1,637	29%	22%	26%
1,856	20%	25%	22%
1,857	20%	24%	22%

*Percentage of total sequences in which individuals can be identified for each medium (video, n = 520; visual, n = 420; total, n = 940).
[a]Identified by studbook number.

per sequence occurring on natural substrates (Table 3). This indicates that locomotion on natural substrates was not overrepresented because it may have been noisy and attention-getting, nor was it underrepresented due to visual obstructions.

Data were transcribed onto checksheets before entry into a spreadsheet. As observational and video methods have been shown to be comparable in content [Rosenberger and Stafford, 1994, Tables 2 and 3], we combined data from both in the analysis. Raw scores were converted to daily percentages based on the total number of bouts and substrate uses observed each day. The coefficient of variation was used as a measure of behavioral variability [e.g., Beckoff, 1977; Sokal and Rohlf, 1981].

Locomotor bouts were classified according to footfall pattern [Rosenberger and Stafford, 1994], whereas substrate was categorized in terms of size and inclination (Table 4). Substrate size was determined functionally in reference to the anatomy of *L. rosalia* [using Hershkovitz, 1977, for measurements], particularly with regard to their capacity to clasp supports with the arms and grip branches with the hands and feet. Dimensions were not assigned to substrate categories until after their definition. This procedure enabled us to define substrate categories of possible functional significance to the animals and to record observations consistently due to the presence of an independent scale in the observations, namely, the animal. Support inclination was recorded as horizontal (< 30°), diagonal (30–60°), or vertical (> 60°).

RESULTS

The locomotor profile of the animals in Beaver Valley is presented in Table 1, which shows the frequencies of locomotor bouts over the course of the study. Arboreal quadrupedal walking (32%) was the predominant locomotor style, followed by leaping (18%), vertical climbing (15%), and equal amounts of bounding (12%) and quadrumanous climbing (12%). The basic themes of locomotion were variations of quadrupedalism (i.e., walking + bounding + quadrumanous climbing = 56%), in contradistinction to saltatory behaviors (leaping + bounding leaps = 23%). This confirms the classification of *L. rosalia* as basically quadrupedal in captivity [Rosenberger and Stafford, 1994]. The supports most frequently used (73%; Table 1) were small enough to be grasped by the animal, i.e., ropes (31%), hand-size branches (No. 4, 21%), and smaller, finger-size twigs (No. 5, 21%). Larger supports were rarely used.

The relationship between locomotion and substrate is illustrated in Table 5. Many locomotor styles appear associated with specific substrate classes, as noted for

TABLE 3. Number of bouts per sequence recorded on and off ropes

	Video		Visual		Total	
	Rope	Natural	Rope	Natural	Rope	Natural
N[a]	344	464	104	196	448	660
Mean[b]	2.13	2.39	2.6	2.9	2.37	2.68
CV	78	81	60	85	69	83

[a]Number of locomotor sequences utilizing exclusively ropes or natural substrates.

[b]Number of bouts per sequence.

TABLE 4. Locomotor categories and substrate classes

Locomotor categories

Quadrupedal walking: Pronograde quadrupedal progression using a diagonal sequence gait, including "running."

Quadrupedal "transaxial" bounding: A transverse gallop with extended suspension characterized in *L. rosalia* by unique hand and foot placements (see Rosenberger and Stafford, 1994, for a detailed discussion of this behavior).

Quadrumanous climbing: Quadrupedal progression among small terminal branches where an animal's weight is spread across more than one support.

Leaping: Saltation from a stationary posture.

Bounding leap: Saltational extensions of quadrupedal walking or bounding, as when crossing between supports, or passing bends or obstructions.

Vertical climbing: Ascent of a steeply inclined (> 60°) support.

Suspension: Walking suspended below a support, or hindlimb suspension when it is used to cross between supports.

Substrate classes

No. 1: Vertical trunks below the canopy, too wide for the animals to reach halfway around with their forelimbs (> 30 cm in diameter).

No. 1a: Vertical trunks below the canopy that the animals can reach halfway around (~12.5–30 cm in diameter).

No. 2: Boughs within the canopy of any angular orientation (~12.5–30 cm in diameter).

No. 3: Canopy or subcanopy branches approximately the same diameter as the animals shoulder width (~5–~12.5 cm in diameter).

No. 4: Canopy or subcanopy branches that a tamarin can encircle with the hand (~1.5–~5 cm in diameter).

Rope: The 2.5 cm diameter manila rope.

No. 5: Canopy or subcanopy supports about which the animals could curl their fingers, generally a terminal branch (<~1.5 cm in diameter).

wild *Saguinus* [Garber, 1991]. Walking and bounding were strongly associated with rope use; quadrumanous climbing, and suspension with terminal supports (Nos. 4 and 5); and vertical climbing with vertical understory supports (Nos. 1 and 1a).

There was, however, a high degree of variability in behavior and substrate use (Table 1), which makes it difficult to interpret differences between sampling periods as real changes in locomotion. This high degree of variability may be explained by factors such as foraging and exploring, or regimented provisioning and interactions with visitors. It may also reflect the novelty and/or challenge of the arboreal experience for cage-reared monkeys. Locomotor behavior appeared to have been less variable than substrate use over the course of the study with coefficients of variation

TABLE 5. Relationships between locomotion and substrate*

	AQW (1,156)[a]	AQB (432)	AQCb (307)	L (515)	BL (184)	VCb (570)	Su (84)
1	0%	0%	0%	7%	12%	35%	0%
1a	0%	0%	0%	7%	3%	32%	0%
2	1%	0%	1%	4%	2%	8%	0%
3	8%	7%	3%	12%	13%	7%	5%
4	27%	13%	19%	29%	28%	12%	35%
Ro	47%	77%	3%	17%	34%	0%	19%
5	18%	3%	75%	23%	7%	6%	41%

*Explanation: AQW, arboreal quadrupedal walking; AQB, arboreal quadrupedal bounding; AQCb, arboreal quadrumanous climbing; L, leaping; BL, bounding leaping; VCb, vertical climbing; Su, suspension. 1, vertical trunks, greater than armspan in diameter; 1a, vertical trunks, armspan in diameter; 2, boughs armspan in diameter; 3, branches, shoulder width; Ro, rope; 4, branches, hand width; 5, terminals; (see text for further descriptions).

[a] Numbers in parentheses represent the total number of bouts for each locomotor category.

(CV) ranging from 19–81 (average = 43, Table 1), whereas the CV values for substrate classes were 34–76 (average = 55). This disparity may reflect morphological constraints on locomotor behavior. Thus in spite of consistent associations between locomotion and substrate classes (Table 5), behavior may be more predictable—due to morphology—than substrate use.

The number of bouts per locomotor sequence remained relatively constant between observation days, averaging 3.16 (s.d. = 0.90, range = 2.43–5.42), and the number of bouts per sequence occurring exclusively on ropes compared to those occurring off the ropes are no different (Table 3). We had expected that there would be a greater number of bouts per sequence in the tree crowns and understory due to their more complex geometric structure. These data may indicate that the animals perceive of and interact with their environment in terms of discrete units of movement that are relatively fixed.

A comparison of the locomotion of *L. rosalia* at Beaver Valley with that of *L. rosalia* at the Conservation and Research Center (CRC) [Rosenberger and Stafford, 1994], shows that although general categories of locomotion are comparable between the two sites (Fig. 1), walking replaces bounding as the dominant locomotor category at Beaver Valley. This we attribute to the differential character of the substrates available to the animals.

DISCUSSION

Functionally, the limb proportions of *Leontopithecus*, with an intermembral index (forelimb length/hindlimb length × 100) of 88, are consistent with their classification as a basically quadrupedal primate [Fleagle, 1988; Rosenberger and Stafford, 1994]. However, with grappling claws and small body size (head and body length 255 mm; weight 665 g), the body plan of *Leontopithecus* also conforms to that of a leaper [Garber, 1991]. The Beaver Valley data suggest that *L. rosalia* preferentially use small-size supports for movement and tend to incorporate leaping and vertical climbing, rather than suspensory locomotion, into their quadrupedal repertoire. This is consistent with their relatively small size: leaping is a critical method for

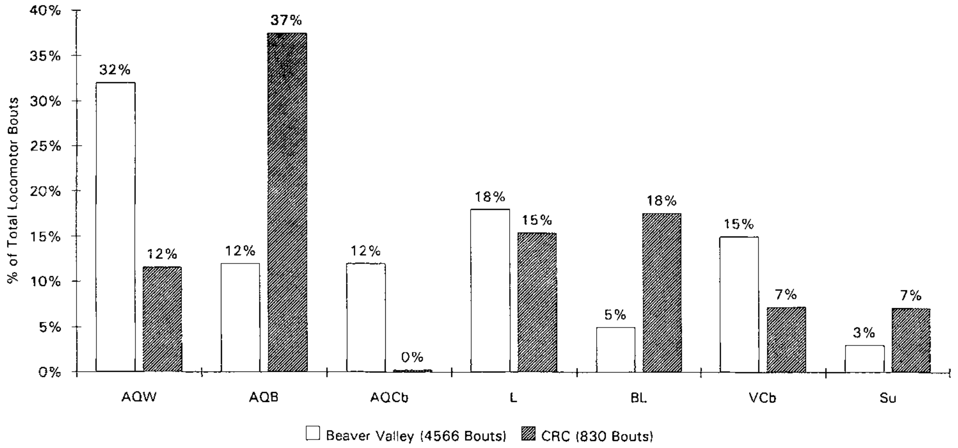

Fig. 1. Comparison of the locomotor profiles of *Leontopithecus rosalia* at Beaver Valley NZP, and at CRC. AQW, arboreal quadrupedal walking; AQB, arboreal quadrupedal bounding; AQCb, arboreal quadrumanous climbing; L, leaping; BL, bounding leaping; VCb, vertical climbing; Su, suspension.

crossing the multitude of relatively large gaps encountered by a small bodied species while moving within a complex, discontinuous arboreal milieu. Some wild callitrichines, such as *Saguinus*, encounter these gaps in the canopy [Garber, 1991], whereas others such as *Cebuella* and *Callimico* encounter these gaps in the understory [Kinzey et al., 1975; Pook and Pook, 1981]. At Beaver Valley, where vertical supports conducive to leaping in the understory are sparse, and ropes provide continuous pathways in the subcanopy, leaping represents a preferred way of moving through small terminal supports (Nos. 4 and 5 in Table 5).

In a parallel study [Rosenberger and Stafford, 1994] using the same methodology to examine locomotion in *L. rosalia* housed in very different captive conditions, we found a different locomotor profile (Fig. 1). The CRC environment consisted of relatively large outdoor enclosures (7 m L × 3.5 m W × 2.4 m H) with nearly all supports horizontal, firm, and of medium-to-large diameter, comparable to the No. 2 and No. 3 supports of Beaver Valley. Based on 830 bouts, the predominant pattern of locomotion in these enclosures involved quadrupedal transaxial bounding and bounding leaps, a low incidence of walking, and negligible amounts of quadrumanous climbing.

We attribute these differences to the contrasting environments of the two sites and to a reciprocal relationship between walking and bounding. These behaviors may present alternative solutions to the differential stability and character of substrates. The higher incidence of bounding and bounding leaps in the CRC enclosures (Fig. 1) appears to be a function of supports that are large in diameter, horizontal, inflexible, long, and uninterrupted. The low incidence of quadrumanous climbing may also reflect the absence of small, closely spaced, and vertically layered supports. Conversely, the higher incidence of walking at Beaver Valley may be related to the majority of supports being smaller, unstable, and interrupted by radial branches. The higher incidence of quadrumanous climbing, in turn, probably reflects the presence of a structured terminal branch microhabitat to which this pattern is suited.

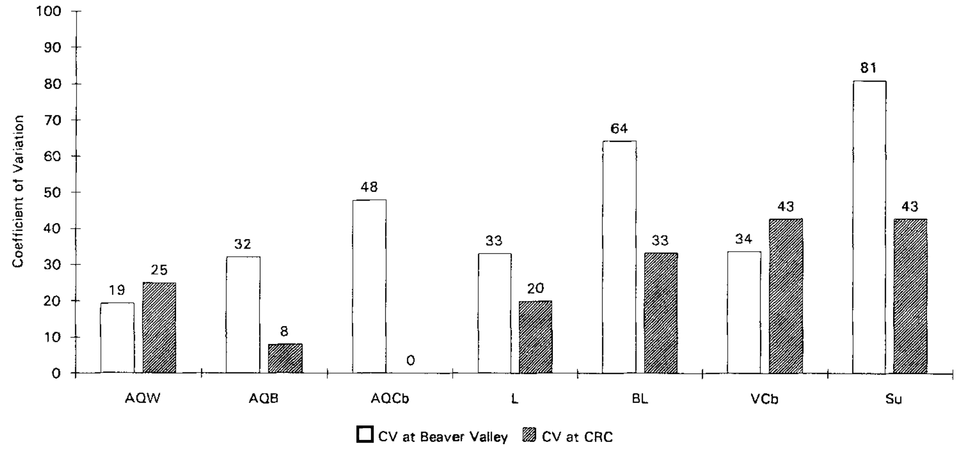

Fig. 2. Comparison of variability in locomotor categories at Beaver Valley NZP, and at CRC. AQW, arboreal quadrupedal walking; AQB, arboreal quadrupedal bounding; AQCb, arboreal quadrumanous climbing; L, leaping; BL, bounding leaping; VCb, vertical climbing; Su, suspension.

We had predicted [Rosenberger and Stafford, 1994] that the more variable, treed habitat of Beaver Valley would elicit more leaping than the conventional enclosures. However, comparable amounts of leaping (Fig. 1) occurred in both settings. This may be due to the placement of the ropes in Beaver Valley, which provided uninterrupted routes through the understory. The CVs for locomotor bouts (Fig. 2), however, are higher at Beaver Valley than at CRC, presumably reflecting the increased complexity of the Beaver Valley habitat. Thus from the viewpoint of an intraspecific comparison, Beaver Valley and CRC animals each behaved in accordance with their substrate options.

Price [1992] described how the behavior of captive-born *Saguinus oedipus* changed after release into an arboreal environment. She emphasized that important adjustments were made during the first 10 weeks of her study, including increases in use of space, arboreal strata, frequencies of moving and foraging, use of oblique and vertical supports, time spent on smaller supports, and a decline in falls. Our study of locomotor behavior and substrate use in *L. rosalia* does not present a convincing picture of change. The behavior of our group remained highly variable throughout the course of study, possibly indicating an intrinsic capacity to adjust to immediate environmental circumstances.

In a field study of positional behavior, Gebo [1992] noted that collection of 3,000 locomotor bouts represented a threshold after which the addition of more data has little effect on the frequency distribution of behaviors. Our overall data set meets this threshold (N = 4566). However, since our daily observation periods only produced 102–496 bouts, well below this threshold, we caution against too strict an interpretation of the temporal data (Table 1) as evidence that *locomotor skills improved per se,* even though this agrees with our preconceptions. Given the high degrees of variability in this data set, it is difficult to know whether the apparent changes in substrate usage and locomotion stemmed merely from exposure to a new environment or from some improvement in locomotor competence.

The inclusion of an arboreal experience as preparation for reintroduction seems to benefit *L. rosalia* when they are returned to the wild [Beck et al., 1991]. Presumably, this is due to the experience they gain in utilizing unfamiliar and unstable supports and to increased biomechanical experience, wherein parts of their locomotor repertoire that are normally underused in captivity become exercised. Kinematic and energetic comparisons with wild-born groups will be required to assess the relative ''quality'' of arboreal locomotor performance in *L. rosalia* and to determine if captive and reintroduced animals move in different ways than wild-born animals.

With regard to the architecture of Beaver Valley, it was unclear from this study whether or not the animals benefited from the rope bridges. Ropes were positioned strategically to encourage movement between large trees, and animals made extensive use of them. However, when two ropes were removed, the animals readily employed alternative natural pathways that were rarely used previously. The styles of locomotion most preferred for crossing ropes, quadrupedal walking, and especially bounding (Table 5), appeared to decrease as rope use declined over the course of the study. Whether or not this was the result of removing two ropes midway through the study is difficult to say, but it does point to the close associations between locomotor styles and available substrate classes.

A high frequency of quadrupedal transaxial bounding appears to be an artifact of captivity [Rosenberger and Stafford, 1994], as a result of substrate structural homogeneity and a lack of environmental complexity. The high frequency of transaxial bounding at CRC (38% of all bouts, Fig. 1) and its predominance during rope use in Beaver Valley (77% of all bounding, Table 5) indicates that the presence of long, uninterrupted, horizontal supports may promote high frequencies of this behavior. Transaxial bounding is observed at much lower frequencies in the wild.

The presence of ropes in Beaver Valley did not appear to affect the animals' ability to access any part of the forest. However, Redshaw and Mallinson (1991) note that free-ranging *L. rosalia* did not use the ropes provided in their study and termed them ''unsuitable'' as substrates for this species. Although there are clear advantages to employing ropes in a free-ranging context, to afford optimal observation conditions or provide the animals access to distant areas of the habitat, it is our concern that artificial substrates may enhance atypical locomotor behaviors. This highlights the need for care when attempting to structure a captive environment in an effort to elicit more naturalistic behaviors.

CONCLUSIONS

1. Free-ranging captive *Leontopithecus rosalia* exhibit a basically quadrupedal locomotor profile incorporating both leaping and vertical climbing as important but less frequent components.
2. Locomotor differences between free-ranging *L. rosalia* and groups inhabiting unenriched enclosures are attributed to differences in available substrate structure.
3. There are strong associations between specific locomotor behaviors and substrate classes, although both remain highly variable even after prolonged exposure to an environment.
4. The implementation of locomotor behaviors may be less variable than the use of substrate classes and may be constrained by morphology.
5. Comparative studies of species in different contexts provides a method for

identifying potential stereotypies, such as the high frequency of transaxial bounding in *L. rosalia* in captivity.

6. The inculcation of a captive locomotor profile does not necessarily inhibit the general ability of captive-born animals to move through the forest.

ACKNOWLEDGMENTS

We thank colleagues and supporters of the Golden Lion Tamarin Conservation Program, especially Dr. D.G. Kleiman at the National Zoological Park and Dr. J. Dietz at the University of Maryland; financial support from the Smithsonian Institution's International Expeditions and Special Programs and Scholarly Studies Program, Friends of the National Zoo, Brookfield Zoo (Chicago Zoological Society), the World Wildlife Fund For Nature-WWF, National Geographic Society, TransBrasil Airlines, and IBAMA; Shauna Keane for assistance in data collection; and Dr. Kaci Thompson for assistance and tolerance in editing this manuscript. B.J.S. especially thanks Betty and John Stafford for their unwavering and continued support and encouragement.

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