LOCOMOTION OF GOLDEN LION TAMARINS (*Leontopithecus rosalia*)

The Effects of Foraging Adaptations and Substrate Characteristics on Locomotor Behavior

Brian J. Stafford,[1]* Alfred L. Rosenberger,[2] Andrew J. Baker,[3]
Benjamin B. Beck,[2] James M. Dietz,[4] and Devra G. Kleiman[2]

[1]Department of Anthropology
City University of New York
33 West 42nd Street
New York, New York 10036
and New York Consortium in Evolutionary Primatology
[2]Department of Zoological Research
National Zoological Park
Smithsonian Institution
Washington, DC 20008
[3]Curator of Small Mammals and Primates
Philadelphia Zoological Gardens
Philadelphia, Pennsylvania 19104
[4]Department of Zoology
University of Maryland at College Park
College Park, Maryland 20742

INTRODUCTION

Our study of the locomotor behavior of golden lion tamarins (*Leontopithecus rosalia*) was initiated because these unique, highly endangered primates, were perceived to possess locomotor deficiencies upon reintroduction to the wild. The critical status of the wild population (Coimbra-Filho and Mittermeier, 1978, Kleiman *et al.*, 1986) led to the establishment of the Poço das Antas Biological Reserve 70 km outside of Rio de Janiero in 1974. The reserve consists of approximately 5000 ha of disturbed lowland rainforest

---

*Current address to which correspondence should be addressed: Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008.

Adaptive Radiations of Neotropical Primates
edited by Norconk *et al.* Plenum Press, New York, 1996

(Kleiman *et al.* 1986, 1991; and Rylands, 1993 for details on reserve condition and environment). A program of reintroductions designed to resupply the declining wild population (Beck *et al.*, 1991; Kleiman, 1989; Kleiman *et al.*, 1986, 1991) by culling social groups from the world's captive stock was initiated in 1984. The first reintroductions, although successful, raised concerns that captive animals released into the forest may exhibit locomotor, and other behavioral deficiencies resulting from their lack of experience in such a complex environment (Kleiman *et al.*, 1986). Thus, a program of prerelease and postrelease training was designed to aid in the transition of captive-born animals into the wild. The research program reported in this paper was conceived to describe and quantify locomotion in *L. rosalia* with these issues in mind.

This report summarizes the first phase of this project, consisting of three separate but interrelated studies. First, a description and quantification of the locomotor behavior of captive animals housed in conventional enclosures; second, a companion study of captive animals newly released into a free-ranging setting at the National Zoological Park; and third, an initial field study of locomotion in wild *L. rosalia*. These studies were designed to allow a comparison of locomotion across these groups to determine the degree to which positional behavior of captive individuals differs from that of wild animals. During the first study (Rosenberger and Stafford, 1994), comparisons were made with captive Goeldi's monkeys, *Callimico goeldii*, housed in the same enclosures with the *L. rosalia* in order to gain taxonomic perspective on locomotion in callitrichines (*sensu* Rosenberger, 1979). Only data on *L. rosalia* are included here.

One of our main goals has been to separate behaviors related to the adaptations of the wild population from those resulting from the effects of captivity. Another was to evaluate the effects of differences in substrate structure on locomotor behavior in order to determine how these variables affect the locomotor profile. Throughout this study we consider morphology to be constant across our groups of *L. rosalia* since our investigations (Stafford and Rosenberger, in prep) do not indicate morphological differences between captive and wild animals for the characters considered here.

We were able to identify two factors that affect locomotion in *L.* rosalia. The first of these was related to substrate structure. These effects are difficult to evaluate between wild and captive groups because of the different ontogenetic experiences of captive and wild animals, as well as the differences in substrate availability between captive and wild settings. The second set of effects relates to the expression of locomotor patterns which we hypothesize are circumscribed by morphology, and therefore related to the phylogenetic experiences of the species.

METHODOLOGY

We studied four social groups of *L. rosalia* (Table 1), two captive-born and two wild-born. Details of group composition, housing and substrate setting for the two captive groups were discussed in detail elsewhere (Rosenberger and Stafford, 1994; Stafford, Rosenberger, and Beck 1994) and will only be summarized here. The CRC group lived in conventional cinder block enclosures, in mixed housing with several groups of *Callimico*, at the Smithsonian Institution's Conservation and Research Center (CRC) in Front Royal, Virginia. They occupied indoor and outdoor cages, furnished by a substrate network of mostly horizontal branches, roofed and fronted with standard cyclone fencing. Supports were arranged in a grid pattern four feet off the floor with one or two vertical or diagonal supports providing access to the cage floor. Animals were only observed in the outdoor

Table 1. Study groups

	Number of Adults	Number of Bouts
Conservation and Research Center (CRC)		
Leontopithecus rosalia	4	825
Callimico goeldii	14	1197
Beaver Valley, National Zoological Park (NZP)	5	3338
Poço das Antas Biological Reserve (PDA)	8	3795

enclosures for consistency across study groups. The Beaver Valley group consisted of five *L. rosalia* newly released into a forested area in the National Zoological Park (NZP) for the first time. This area consists of about 0.2 hectares of mature beech and oak forest forming a continuous canopy, and an understory below three meters of shrubs and bushes. A network of hemp ropes was strung up in the subcanopy, connecting the centrally located nest box to the perimeter of the site. Wild *L. rosalia* were studied at the Poço das Antas Biological Reserve (PDA) in Brazil and were observed over 19 days for a total of 76 hours. This resulted in the collection of 3795 locomotor bouts.

Data were recorded using a modified focal animal sampling method (Altmann, 1974; see Rosenberger and Stafford, 1994; or Stafford *et al.*,1994 for details of our particular method) for all groups. Visual observations were supplemented by videotapes recorded under the same protocols as visual sampling. Our unit of observation was a locomotor sequence, which we defined as a string of locomotor bouts proceeding without a postural interruption of more than 3–5 seconds. The locomotor bout, in turn, was defined by the maintenance of a single locomotor pattern across a single class of supports. This convention is required because locomotor behaviors (e.g., walking) may be performed differently on supports of different size or orientation. Locomotor categories were based on detailed observations of how the animals moved, and considered within the framework of discrete behaviors as described by Hildebrand (1967, 1977, 1980). This methodology allowed us to distinguish gait patterns between species, and to discern differences within gait categories.

We find this approach most instructive due to the transient nature of the taxonomy of primate locomotion (see Prost, 1965; Martin, 1990; Napier and Walker, 1967; Rose, 1973; Fleagle, 1988 for examples of how the terminology associated with primate locomotor studies has changed over the years). A functional and kinematic approach to defining locomotor behaviors (as advocated by Prost, 1965; and Hildebrand, 1967) should ensure relative constancy in the delineation of discrete behaviors over time. Also, since we are interested in discovering anatomical correlates of locomotion that will be useful in interpreting the fossil record, we believe that a kinematically based definitional system (as advocated by Prost, 1965) provides the most powerful methodology for linking behavior and morphology.

We have argued (Rosenberger and Stafford, 1994) that some features of the skeleton in *L. rosalia* are linked to gross interspecific differences in locomotor behavior while other characters affect the system more subtly. For this reason it is important to understand the information content of one's observations and throughout this report we consider our locomotor variables at two levels. The first level is that of the generalized locomotor profile in which locomotor behavior is grouped into larger conceptual categories (Table 2). The second is a finer grained analysis, in which the components of the generalized profile are broken down into more specifically defined subcategories for consideration. A

Table 2. Locomotor categories and substrate classes

Locomotor Categories

Specific 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.

Saltatory 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 ($>60^{0}$) support.

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

Gap Bridging: Crossing between two discontinuous supports by placing some combination of limbs in contact with the target support before transfering the body accross the gap.

General Locomotor Categories[1]:

Quadrupedalism-g: Walking + Bounding + Climbing.

Leaping-g: Leaping + Bounding Leaping.

Vertical Climbing-g: Vertical Climbing.

Suspensory-g: Suspension + Gap Bridging.

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 which 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).

Terrestrial: Cage or forest floor.

Substrate Orientation

Horizontal: Substrates between 0^{0} and 30^{0} inclination.

Diagonal: Substrates between 30^{0} and 60^{0} inclination.

Vertical: Substrates between 60^{0} and 90^{0} inclination.

Forest Level

Canopy: Locomotion above the level at which branches begin to spread from the trunks of the trees forming an interlocking layer.

Subcanopy: Locomotion between the canopy and above two meters from the ground.

Below 2 Meters: Locomotion within two meters of the ground.

Terrestrial: Locomotion on the forest floor, or floor of the cage.

---

[1] General locomotor categories are distinguished from specific categories of the same name by adding the suffix -g.

comparison of these two levels of resolution offers valuable insight into the application of functional analyses based on extant taxa to the fossil record.

Table 2 provides definitions of our locomotor and substrate categories. Some familiar categories were lumped together here when we could not distinguish between them consistently, or because of their usage in earlier phases of this project. For example, "vertical climbing" as presented here is actually composed of two distinct behaviors, vertical climbing and vertical bounding. In vertical climbing the animal is ascending or descending a vertical support with diagonal hindlimbs and forelimbs moving in synchrony. In vertical bounding, however, the forelimbs move in synchrony with each other, as do the hindlimbs. Because these behaviors were not distinguished during our initial study at CRC due to substrate availability at this site (i.e., only a few short supports were available for this behavior), we lump them into one category for comparison. A second instance of combining categories involves our walking category, which includes both walking and running. Both of these gaits utilize a diagonal couplets, diagonal sequence footfall formula. The difference between walking and running relates to the amount of time each limb retains contact with the substrate (see Hildebrand, 1967 for more complete descriptions). Operationally, this translates into how fast the animal is moving, i.e., walking is slower than running. Because we could not distinguish the transition between these two gaits during observations, we classified them together as walking. General locomotor categories are composites of more rigidly defined specific locomotor categories, and are identified by the suffix -g.

Substrate diameters were determined in relation to the size of the animal and the manner in which the animal used the support, especially how the animal grasped a support. We decided on this approach because of theoretical expectations that an animal walking on a 10 cm diameter support that cannot be grasped with the hand will move differently than it would when walking on a 2 cm diameter support that can be grasped. To what degree this is true has yet to be determined through kinematic analysis, but analysis of videotapes indicates that hand and foot placements and general body orientation are different on substrates of different sizes. This method of estimating substrate size also offers the observer a built-in scale when collecting data, namely the animal itself. As a result, we are very confident in our assignment of substrate sizes between sites presenting very different viewing conditions.

Our forest level categories deserve special mention. We divided the habitats of the animals into four levels based, in part, on geometry and continuity of supports (see Table 2). The canopy and subcanopy can be distinguished by the presence of interconnected branches in the canopy. The subcanopy, however, is dominated by the vertical trunks of the trees and presents a less continuous environment. The terrestrial level is self explanatory, and our "below two meters" category reflects the fact that wild *L. rosalia* appear to spend a good deal of time close to the forest floor, scanning the leaf litter for invertebrate prey items. The specific height of two meters was chosen because it could be reliably and repeatedly identified by observers. In fact, throughout our entire study, *L. rosalia* were seldom seen scanning for terrestrial prey from a height above two meters. Therefore, only this category and terrestriality legitimately represent the height of the animal. The habitat structure at the Poço das Antas reserve is extremely variable, ranging from areas similar in structure to old growth forest to areas of open grasslands. As a result, in some parts of the reserve the structural subcanopy may extend above the height of the canopy found in other parts of the forest. Tall stands of bamboo are one such example which we would consider not to have a canopy level. Therefore, our concept of forest level is one of structure, geometry, and substrate continuity, and has little or nothing to do with how high above the ground the animals actually were.

Table 3. Results of analysis of variance

General Locomotor Categories

	Quadrupedalism	Leaping	Vertical Climbing	Suspension
CRC vs NZP	NS	**	*	NS
CRC vs PDA	**	NS	**	**
NZP vs PDA	**	**	NS	*

Specific Locomotor Categories

	Walking	Bounding	Climbing	Leaping	Bounding Leaping	Vertical Climbing	Suspension	Gap Bridging
CRC vs NZP	**	**	**	NS	**	*	**	NS
CRC vs PDA	NS	**	**	*	**	**	**	NS
NZP vs PDA	**	NS	NS	**	NS	NS	NS	NS
NZP vs PDA-rope	**	**	NS	**	NS	NS	NS	NS

Substrate Classes

	Trunks >30 cm	Trunks 12.5-30 cm	Branch 12.5-30 cm	Branch 5-12.5 cm	Branch 1.5-5 cm	Rope	Branch <1.5 cm	Terrestrial
CRC vs NZP	*	**	**	**	**	**	**	NS
CRC vs NZP-rope	*	**	**	**	**	NA	**	NS
CRC vs PDA	*	**	**	**	**	NA	**	*
NZP vs PDA	**	NS	NS	**	**	**	NS	NS
NZP vs PDA-rope	**	NS	NS	**	NS	NA	NS	NS

Substrate Orientation

	Horizontal	Diagonal	Vertical	Terminals
CRC vs NZP	NS	*	**	*
CRC vs PDA	**	NS	**	**
NZP vs DA	**	**	**	**

Forest Level

	Canopy	Subcanopy	Below 2 meters	Terrestrial
CRC vs NZP	NS	**	**	*
CRC vs PDA	**	**	**	**
NZP vs PDA	*	**	NS	NS

*p<0.01; **p<0.001; NS = not significant; NA = not applicable

Spearman's rank correlation (r) was used to test for significant correlation between locomotor, substrate size, substrate orientation, and forest level profiles between groups. Correlations were considered to be significant when $p<0.01$. To test for difference between individual components of these profiles we used pairwise single classification analysis of variance. Here, categories were considered to be significantly different when $p<0.01$.

THE MAJOR FEATURES OF LOCOMOTION IN *Leontopithecus rosalia*

Figure 1 shows the general locomotor profiles of *L. rosalia*. At CRC we find that *L. rosalia* is basically quadrupedal with leaping of secondary importance. Suspension and

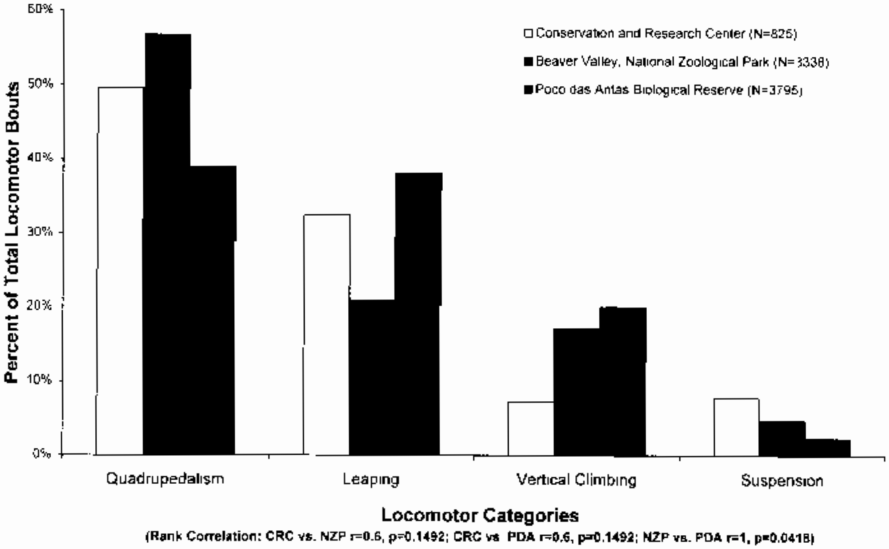


Figure 1. Locomotion of *Leontopithecus rosalia* (general locomotor categories).

vertical climbing represented less significant components of the locomotor profile. These generalizations are consistent with differences in limb indices between *L. rosalia* and *Callimico* (Rosenberger and Stafford, 1994) (Table 4), with forelimb and hindlimb lengths more nearly equal in *Leontopithecus* while *Callimico* has appreciably longer hindlimbs. Given this, one would expect more quadrupedalism in *Leontopithecus*. Data collected from the videotapes (Figure 2) showed that *L. rosalia* typically utilize the transverse gallop, a gait which involves a marked overstriding of the forelimbs by the hindlimbs. Such a condition is not unique for primates (see Hildebrand, 1967; Tuttle, 1969; and Vilensky, 1989; Vilensky and Larson, 1989) or even for mammals that gallop, but it does appear to be unique to *Leontopithecus* among the callitrichines. This may be the result of the incorporation of elongate forelimbs into the locomotor system. As shown in Figs. 2 and 3, *L. rosalia* use a unique pattern of hand and foot placement when galloping. Rather than positioning the hands and feet on either side of a support, both forelimbs and hindlimbs are set to one side. We have proposed the term "transaxial bounding" (Rosenberger and Stafford, 1994) to describe this pattern because although the gait is technically a gallop it fulfills the role of rapid quadrupedal locomotion in *L. rosalia* where other callitrichines utilize a half-bound.

We first identified transaxial bounding at CRC, and initially thought it represented an artifact of captivity but since then we have confirmed the occurrence of this pattern in wild-born *L. rosalia* at Poço das Antas and also in captive *L. chrysomelas*. To date, we have found no differences in gait patterns between the captive-born zoo animals and the wild animals, although we continue to investigate this possibility. Therefore, transaxial bounding appears to be a normal locomotor pattern in *Leontopithecus*.

Kinematically this gait is quite distinctive. The hindquarters are displaced lateral to the midline of the support before the hind feet contact it (Figure 2b&c). During the next phase of the stride, when the animal is extending the spine (Figure 2a), the shoulders

Table 4. Selected limb indices in callitrichines

Taxon	Mass[2]	STL	IMI[3]	BI[4]	CI[5]	Forelimb[6]	Hindlimb[7]	McI[8]	MtI[9]	TotFore[10]	TotHind[11]
Callimico goeldii	482 g	163 mm	71	92	101	63	89	8.52	14.14	72	103
Saguinus sp.	472 g	167 mm	76	90	101	60	79	8.94	14.39	69	94
Leontopithecus rosalia[12]	495 g	173 mm	88	96	100	74	83	13.25	16.73	87	100
Callithrix jacchus	294 g	139 mm	75	90	102	62	84	8.90	15.78	71	99
Cebuella pygmaea	116 g	93 mm	82	90	102	69	84	9.14	15 24	78	98
t-test[13]		p<.01	p<.01	p<.05	p=.13	p<.01	p=.47	p<.01	p<.01	p<.01	p=.05

[1] Data based on selected records from Dykyj (1982) unless otherwise noted. N = 4 in all cases

[2] Data taken from Rosenberger (1992). More recent data on body weights in wild *L. rosalia* are available in Dietz *et al.* (1994). Ford and Davis (1992) and Ford (1994) provide data for a wider range of platyrrhines.

[3] Intermembral Index = ((Humerus length + Radius length)/(Femur length + Tibia length))*100

[4] Brachial Index = (Radius length / Humerus Length)*100.

[5] Crural Index = (Tibia length / Femur length)*100.

[6] Forelimb Index = ((Humerus length + Radius length) / STL)*100.

[7] Hindlimb Index = ((Femur length + Tibia length) / STL)*100.

[8] Metacarpal Index = (Metacarpal III length / STL)*100.

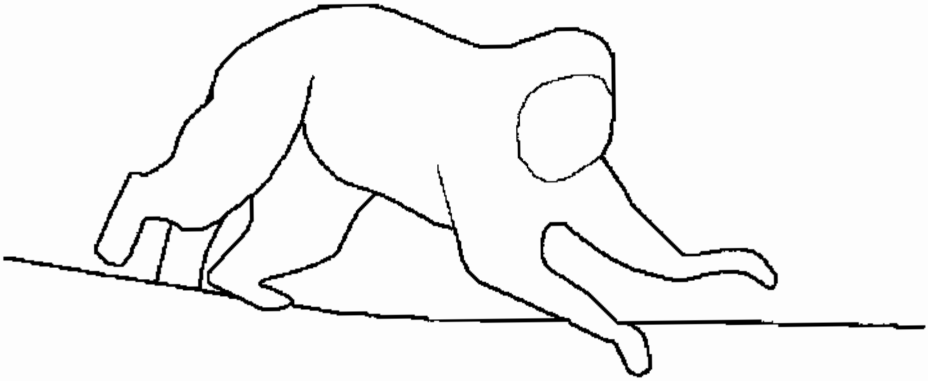
[9] Metatarsal Index = (Metatarsal III length / STL)*100.

[10] Total Forelimb Index = ((Humerus length + Radius length + Metacarpal III length) / STL)*100

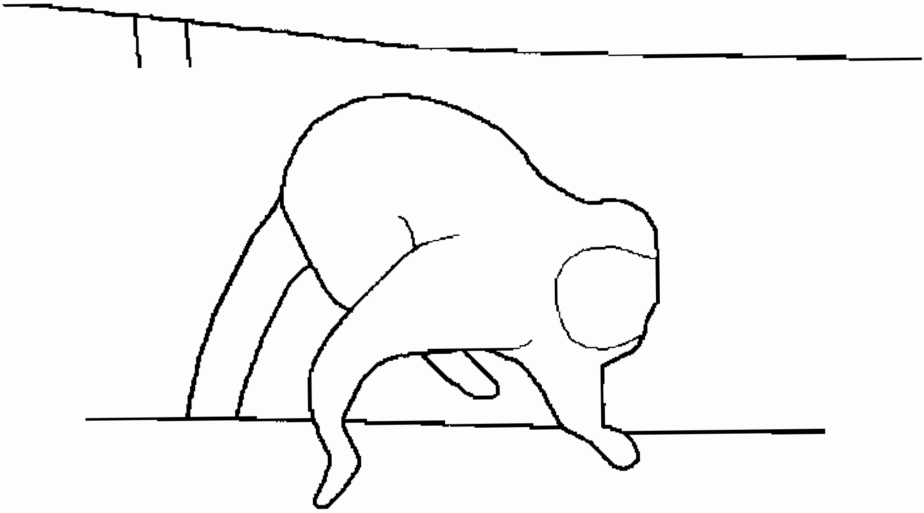
[11] Total Hindlimb Index = ((Femur length + Tibia length + Metatarsal III length) / STL)*100.

[12] Data collected from USNM#s 546317, 546320, 546321, and 546322.

[13] t-test is 1 tailed for samples with unequal variance testing *L. rosalia* against all other taxa. Level of significance is p<.05.



Frame 2 of 13



Frame 6 of 13

Figure 2a and b. Galloping in *L. rosalia* at CRC taken from a sequence of video frames.

straighten out in the direction of travel (Figure 2c) but turn laterally again as the forelimbs contact the substrate (Figure 2a, see Figure 5 Rosenberger and Stafford, 1994). The resulting pattern is visually very distinctive compared to the half-bounding of *Callimico* and produces a situation where the animal's body oscillates back and forth over the midline of the support.

We have suggested (Rosenberger and Stafford, 1994) that the specific pattern of forelimb elongation in *Leontopithecus* contributes to this gait pattern. The proportions of the antebrachium and manus in *Leontopitecus* are unique among callitrichines (Table 4), and indices clearly show that the longer forelimbs in *Leontopithecus* result from the elongation of distal limb segments. Such a condition, with long forelimbs leading to more

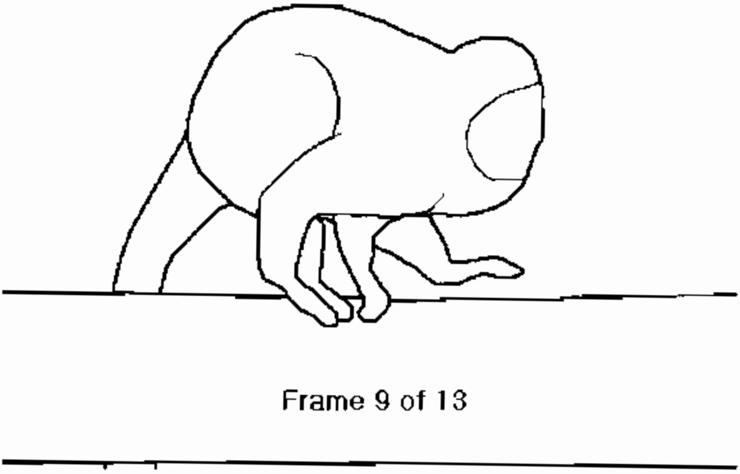


Figure 2c. Galloping in *L. rosalia* at CRC taken from a sequence of video frames.

equal relative limb indices, may impart an advantage to galloping over bounding in *Leontopithecus*. Certainly, this condition would lead to increased arcs of excursion of the body over the forelimb, producing an overstriding gait and increased stride length. These advantages probably explain the common occurrence of overstriding among mammals (i.e., equids, canids, felids, bovids) and primates (*Gorilla*, *Pan*, *Pongo*, or *Cercopithecus*; see Hildebrand, 1967; or Vilensky and Larson, 1989 for examples) that gallop. However, these examples involve either terrestrial cursorial mammals, or primates moving terrestrially. Our observations indicate that other callitrichines (*Callimico goeldii*, *Saguinus oedipus*, *Callithrix argentata*, *Cebuella pygmaea*) never enlist overstriding during bounding (*sensu stricto*) on arboreal supports and, to our knowledge, the only other arboreal mammal documented to utilize hindlimb overstriding on arboreal supports is the northern flying squirrel (*Glaucomys sabrinus*), which overstrides while half-bounding (Hampson, 1965). These animals are also notable for having relatively longer forelimbs than their arboreal nongliding relatives (Thorington and Heaney, 1981), although this elongation does not extend to the manus (Stafford, unpublished data).

We propose that the elongate hands of *Leontopithecus* necessitate transaxial placement as a means of reducing shearing stresses on the elongate manus. This placement may also allow overstriding to occur on arboreal supports because it reduces the possibility of interference between the forelimbs and hindlimbs by displacing the hindlimbs lateral to the midline of the support. Additionally, the oblique placement of the manus may provide enhanced stability through frictional forces and compensate for the loss of pollical grasping in *Leontopithecus*, a consequence of the highly specialized nature of the hand (i.e., manual elongation and interdigital webbing; see Garber, 1992; Hershkovitz, 1977; Rosenberger and Stafford, 1994).

Our observations on other captive callitrichines (*Callimico goeldii*, *Saguinus oedipus*, *Callithrix argentata*, *Cebuella pygmaea*) suggest that half-bounding is the ancestral pattern for callitrichines, and that forelimb elongation is linked with a change from bounding to galloping in *Leontopithecus*. Such an evolutionary transformation incorporates transaxial bounding as an integral aspect of the locomotor system in *Leontopithecus*. We do not deny the possibility that transaxial bounding confers some selective benefit in locomo-

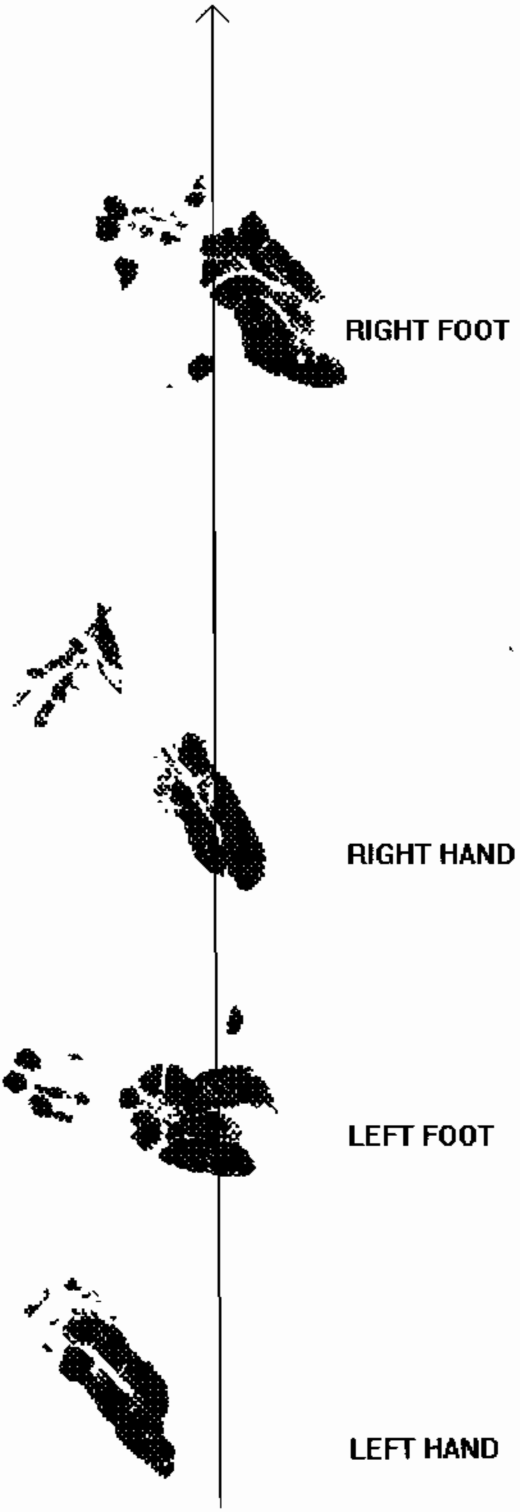


Figure 3. Hand- and footprints of *L. rosalia* galloping at CRC.

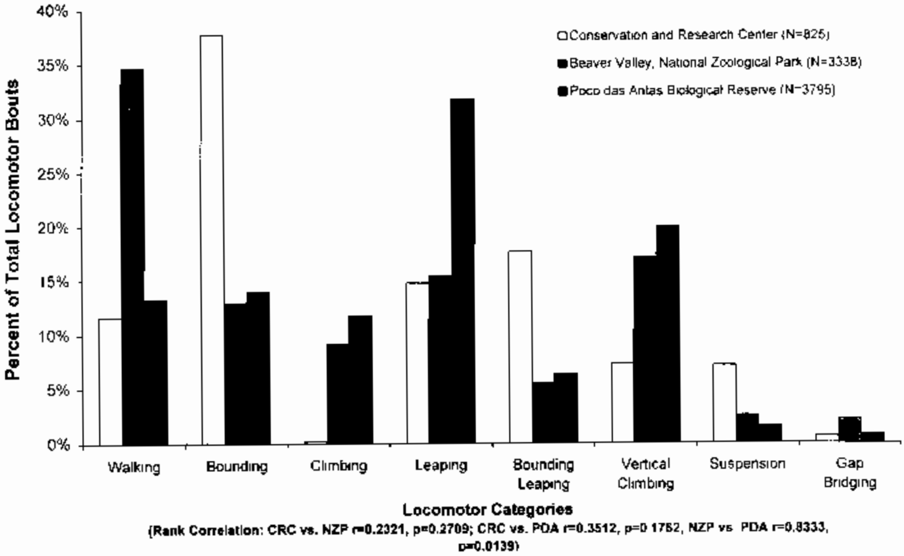


Figure 4. Locomotion of *L. rosalia* (specific locomotor categories).

tor or positional behaviors, but would propose that transaxial bounding is a byproduct of foraging adaptations that are incorporated as integral parts of the skeletal system, not a product of selection for this specific gait pattern.

We prefer the hypothesis that selection for extractive foraging is a better causal explanation of forelimb and manual elongation in *Leontopithecus* (e.g., Hershkovitz, 1977; Rosenberger, 1992) because there is ample biological evidence to support this hypothesis (Peres, 1986; Rylands, 1989). *L. rosalia* rely heavily on concealed, embedded prey which are removed from crevices, holes and the boles of large epiphytes by forceful extraction. Biomechanically, longer forelimbs increase reach and improve leverage. There is also comparative evidence suggesting that the elongation of anatomical components associated with extractive foraging behavior (i.e., phalangeal elongation in *Daubentonia madagascarensis* and *Dactylopsila* sp.; and lingual elongation in *Orycteropus afer*, *Manis* sp., *Myrmecophaga tridactyla*, and *Tamandua* sp., for example) is widespread.

Within the Callitrichinae, forelimb elongation is associated with extractive foraging, galloping, and transaxial hand and foot placement. Extractive foraging provides the most strongly supported hypothesis for the origin of forelimb elongation in *Leontopithecus*, until it can be shown that galloping or transaxial hand and foot placement confer some selective advantage. However, the influence of an elongate forelimb on other aspects of an animal's behavior (i.e., vertical clinging *sensu* Jungers, 1977; Cartmill, 1985; Thorington and Thorington, 1989: leaping Garber, 1991: or quadrupedal locomotion Rosenberger and Stafford, 1994) can have equally important secondary consequences in the daily life of the individual and this may explain the origins of galloping and transaxial hand and foot placement in *Leontopithecus*. It is within this context that we consider the locomotion of *L. rosalia* constrained by morphology.

It should be noted that we may never have identified transaxial bounding had we not studied the animals at CRC. Given the size of these animals, and observation conditions in the wild, it simply is not possible to determine what the animals are doing with their feet. In fact, it required the transplanting of our captive experimental setup into the wild for us to identify transaxial bounding conclusively in wild animals. Furthermore, our ability to recognize transaxial bounding when collecting behavioral observations in the wild relied upon our comparisons of the kinematics of this gait with half-bounding callitrichines. This allowed us to identify characteristics of transaxial bounding that do not rely upon being able to see the animal's feet, and therefore allowed us to identify this behavior reliably in the wild.

CAPTIVE *L. rosalia* IN CONVENTIONAL AND FREE-RANGING ENVIRONMENTS

Locomotor, substrate size, substrate orientation, and forest level usage profiles were not significantly correlated between CRC and Beaver Valley (Figures 1, 4–8), and the differences in locomotion between the two sits were not in accord with our predictions based on our initial work at CRC. We expected that the more discontinuous and flexible substrate conditions at Beaver Valley would elicit more leaping-g and less quadrupedalism-g than we observed at CRC. However, in examining our gross locomotor categories (Figure 1, Table 3) we found exactly the opposite pattern. There was proportionately more leaping-g at CRC, while the frequencies of quadrupedalism-g remained unchanged between the sites.

A more detailed look at locomotion at the two sites (Figure 4, Table 3) also seemed discordant with our predictions. Although quadrupedalism-g was the most frequent category of locomotor behavior at each site, different components of quadrupedalism-g predominated. Animals at CRC showed more ttransaxial bounding, whereas walking dominated at Beaver Valley. Also, bounding leaps occurred with a higher frequency at CRC. This may be explained by the fact that bounding leaping is, by definition, an extension of rapid quadrupedal locomotion (i.e. rapid walking or running, and bounding). We would, therefore, expect more bounding leaping to occur at a site where the animals are doing more bounding. Unexpectedly, saltatory leaping did not differ between the two sites, nor did gap bridging. We would have expected these behaviors to be more frequent in the more varied, unstable, and discontinuous environment at Beaver Valley.

A consideration of substrate character, however, leads to the interpretation (Stafford *et al.*, 1994), that each of the groups was, in fact, behaving in accordance with available substrate options. The animals at CRC were presented with a uniformly continuous, stable, and barrier-free network of supports and as a result they employed more transaxial bounding. In Beaver Valley the animals walked more because they had to negociate more complex and unstable supports. Figure 5 shows the substrate usage profiles for both groups and illustrates the fact that the Beaver Valley group was using smaller, more flexible supports more than was the CRC group. Note specifically that the most commonly used support at Beaver Valley is the rope, which is small in diameter and highly flexible. Consequently, these animals may have been less able to employ transaxial bounding and bounding leaping and opted for walking, a gait which maintains the limbs in contact with the support for a greater percentage of the stride cycle, and is therefore more secure for the animal.

Figure 5 and Table 5 examined together further clarify the differences between the two captive sites. The absence of large vertical trunks, small branches or terminal sup-

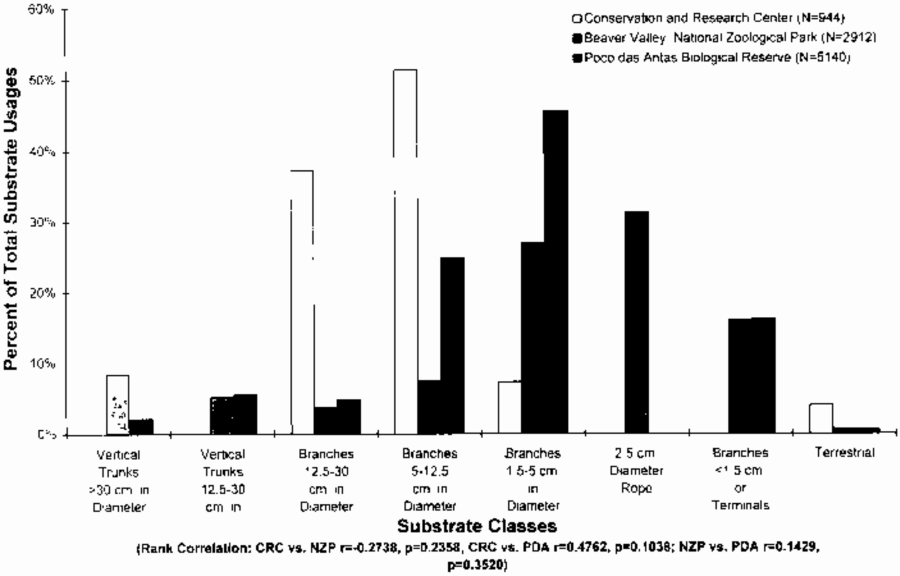


Figure 5. Substrate use by *Leontopithecus rosalia*

ports, and ropes at CRC can immediately account for some differences in behavior. The animals at CRC used larger supports for a majority of their locomotor behaviors while the Beaver Valley animals used the smaller supports in most cases. At CRC there were no close associations between specific locomotor behaviors and specific supports, while in Beaver Valley animals did appear to use specific locomotor behaviors on certain classes of supports. For example, quadrumanous climbing did not occur at CRC but it accounted for 9% of the locomotor profile at Beaver Valley. This can be attributed to the fact that the proper substrates (terminal supports of less than 1.5 cm in diameter) were not present at CRC, while these kinds of substrates were used for 75% of all climbing activity at Beaver Valley (Table 3). Similarly, the greater frequencies of vertical climbing seen at Beaver Valley can be attributed to the presence of large vertical supports in the understory (tree trunks), a class of substrate not available to the CRC animals. The differing character of quadrupedalism between the two sites, however, seems to have less to do with substrate size than with substrate stability (see above). The Beaver Valley animals conducted most of their quadrupedal behaviors on the ropes that were strung between trees in the subcanopy layer (47% for walking, and 77% for bounding).

LOCOMOTION IN WILD AND CAPTIVE *L. rosalia*

The most salient difference between the captive groups and the two wild groups studied (Figure 1, Table 3) is that the captive animals are more quadrupedal than the wild

Table 5. Associations between locomotion and substrate for *Leontopithecus rosalia*

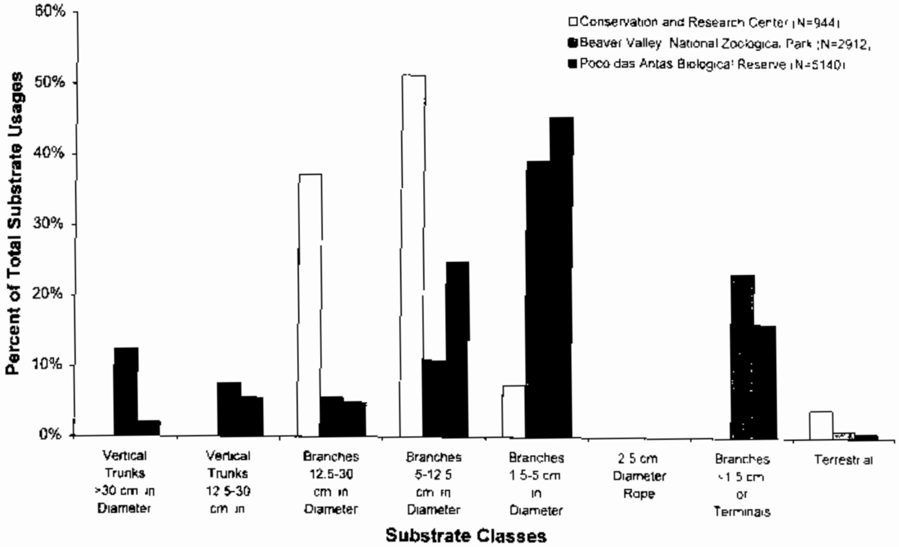
	Walking	Bounding	Climbing	Leaping	Bnd. Leap	VCb	Su&GB
Conservation and Research Center (N=825)							
Vert. trunk >30 cm dia.	0%	0%	0%	0%	0%	0%	0%
Vert. Trunk 12.5-30 cm dia.	0%	0%	0%	0%	0%	0%	0%
Branch 12.5-30 cm dia.	39%	39%	0%	38%	44%	7%	0%
Branch 5-12.5 cm dia.	49%	57%	0%	54%	47%	59%	0%
2.5 cm Rope	0%	0%	0%	0%	0%	0%	0%
Branch 1.5-5 cm dia.	12%	5%	0%	7%	9%	33%	0%
Branch <1.5 cm dia	0%	0%	0%	0%	0%	0%	0%
Beaver Valley, National Zoological Park (N=3338)							
Vert. trunk >30 cm dia.	0%	0%	0%	7%	12%	35%	0%
Vert. Trunk 12.5-30 cm dia.	0%	0%	0%	7%	3%	32%	0%
Branch 12.5-30 cm dia.	1%	0%	1%	4%	2%	8%	0%
Branch 5-12.5 cm dia.	8%	7%	3%	12%	13%	7%	5%
2.5 cm Rope	47%	77%	3%	29%	28%	12%	35%
Branch 1.5-5 cm dia.	27%	13%	19%	17%	34%	0%	19%
Branch <1.5 cm dia	18%	3%	75%	23%	7%	6%	41%
Beaver Valley Minus Ropes (N=2912)							
Vert. trunk >30 cm dia.	0%	0%	0%	10%	17%	40%	0%
Vert. Trunk 12.5-30 cm dia.	0%	0%	0%	10%	4%	36%	0%
Branch 12.5-30 cm dia.	2%	0%	1%	6%	3%	9%	0%
Branch 5-12.5 cm dia.	15%	30%	3%	17%	18%	8%	8%
Branch 1.5-5 cm dia.	50%	57%	20%	24%	47%	0%	29%
Branch <1.5 cm dia	33%	13%	77%	32%	10%	7%	63%
Poço das Antas, Combined Groups (N=3795)							
Vert. trunk >30 cm dia.	0%	0%	0%	2%	1%	8%	0%
Vert. Trunk 12.5-30 cm dia.	0%	0%	0%	6%	1%	16%	0%
Branch 12.5-30 cm dia.	5%	9%	0%	4%	5%	7%	7%
Branch 5-12.5 cm dia.	22%	37%	3%	23%	26%	34%	21%
Branch 1.5-5 cm dia.	59%	48%	31%	46%	54%	33%	41%
Branch <1.5 cm dia	14%	5%	66%	18%	13%	2%	31%
Poço das Antas, Dois Femmes (N=2535)							
Vert. trunk >30 cm dia.	0%	0%	0%	2%	1%	7%	0%
Vert. Trunk 12.5-30 cm dia.	0%	0%	0%	6%	1%	15%	0%
Branch 12.5-30 cm dia.	4%	10%	0%	6%	6%	11%	8%
Branch 5-12.5 cm dia.	20%	35%	4%	24%	26%	33%	20%
Branch 1.5-5 cm dia.	58%	46%	31%	42%	50%	31%	40%
Branch <1.5 cm dia	16%	8%	64%	20%	16%	2%	32%
Poço das Antas, Cacador (N=1260)							
Vert. trunk >30 cm dia.	0%	0%	0%	2%	1%	9%	0%
Vert. Trunk 12.5-30 cm dia.	0%	0%	0%	7%	0%	18%	0%
Branch 12.5-30 cm dia.	6%	9%	0%	1%	5%	0%	0%
Branch 5-12.5 cm dia.	26%	38%	0%	22%	26%	35%	25%
Branch 1.5-5 cm dia.	61%	49%	29%	52%	61%	36%	50%
Branch <1.5 cm dia	7%	3%	71%	14%	7%	2%	25%

animals, while the wild animals use quadrupedalism-g and leaping-g with equal frequency. Although leaping-g appears to occur with comparable frequencies at CRC and PDA, we will see that the nature of this leaping-g is quite different between these two sites. However, vertical climbing-g occurs with comparable frequencies in the wild and at Beaver Valley, but at much lower frequencies at CRC. Surprisingly, suspensory-g behaviors were highest at CRC, lowest in the wild, and intermediate at Beaver Valley. These differences may be the result of the lack of diverse, flexible, and complex substrates at CRC, and reliance of the Beaver Valley animals on the rope bridges. The ropes provide highways through the subcanopy, strung between large vertical supports, a situation that may artificially enhance the frequencies of quadrupedal-g and vertical climbing-g behaviors at the expense of leaping-g behaviors.

A more detailed look (Figure 4) at the locomotor profiles of the captive and wild groups indicates that certain differences between these groups are quite marked (Table 3). Each group of *L. rosalia* exhibited a unique, predominant locomotor preference; transaxial bounding at CRC, walking in Beaver Valley, and leaping at Poço das Antas. The fact that both captive groups predominantly utilize some form of quadrupedalism-g largely explains the differences between the generalized locomotor profiles of the captive sample as a whole and the wild groups. In spite of such large scale differences, the specific locomotor profile of the free-ranging animals in Beaver Valley most closely resembles that of the wild animals. Only two of the eight specific locomotor categories (walking and leaping) differ by more than 3% between the Beaver Valley animals and the wild sample (Table 3). However, between the CRC group and the wild animals only two locomotor categories (walking and gap bridging) are within 3% of each other (Table 3). Furthermore, we now see that the apparent similarity of leaping-g between CRC and PDA is the result of inflated levels of bounding leaping at CRC. In fact, the frequencies of both saltatory leaping and bounding leaping are different between these two sites (Figure 4, Table 3). To this extent, we can confirm that locomotion in the free-ranging environment better approximates the wild than the locomotor behavior exhibited in the cages at CRC.

It is interesting to note that when the effects of rope use are removed from the analysis of Beaver Valley locomotion (Table 3), this group's locomotor profile diverges from that of the wild groups even more. We would have expected the Beaver Valley animals to have more closely approximated the wild groups in such a comparison. However, the locomotor profile of the Beaver Valley animals remains essentially unchanged (i.e. within a few percent of the values for the wild groups in all categories) except that bounding, which now drops to only 3%, is now also significantly different between these groups. Obviously, the fact that 77% of all bounding at Beaver Valley occured on the ropes has a lot to do with this. We interpret these data as evidence that the captive animals are utilizing more conservative gaits on unstable natural supports because even with the exclusion of rope use walking remains disproportionately high at Beaver Valley, while leaping remains low. In effect, the inclusion of rope use in the substrate profile of the Beaver Valley group "artificially" raises the frequency of bounding for this group but does not dramatically affect other behaviors.

Substrate usage profiles (Figure 5, Table 3) were very different between all groups, with the CRC animals showing highly restricted substrate selection and Beaver Valley animals strongly preferring the ropes. The CRC situation is explained by the fact that the animals did not have a diversity of substrates available to them. Because of this, the Beaver Valley substrate profile resembles that at Poço das Antas in indicating a wider selection of substrate types. When the overall profiles are recomputed with the rope category eliminated (Figure 6), the Beaver Valley and the wild samples appear even more similar,



(Rank Correlation: CRC vs. NZP r=-0.1429, p=0.3632; CRC vs. PDA r=0.3571, p=0.1922; NZP vs. PDA r=0.7143, p=0.0410)

Figure 6. Substrate use by *Leontopithecus rosalia* (calculated without ropes).

with branches between 1.5 and 5 cm now no longer statistically different as compared to the wild sample. Interestingly, the exclusion of the ropes from the analysis does not change the relationship between the CRC sample and the Beaver Valley sample, providing further evidence that the Beaver Valley environment elicits behaviors that more closely approximate behaviors seen in the wild.

In both the Beaver Valley and PDA groups, branches that can be grasped in the hand (i.e. 1.5–5 cm in diameter) were the most often used substrates. The Beaver Valley animals used large vertical (>30 cm) trunks much more than did the wild animals and this may be an artifact of the positioning of the ropes, which were strung between large vertical trunks. It is interesting that the Beaver Valley animals appear to use small and terminal branches (<1.5 cm) relatively more than the wild animals once rope use is removed from the analysis, although this change is not statistically significant (Table 3). It is also interesting that the wild animals used larger supports (i.e., ones that are roughly the same diameter as the animal's trunk) more often.

There are two likely explanations for this pattern. The first is that substrate availability is different between the two sites and that the animals are randomly selecting supports based on availability. Testing this hypothesis would require data on relative abundance of substrate types between sites, and such data are not available for these groups. The second hypothesis is somewhat more complex, and proposes that the differences exhibited by our study groups reveal some "deficit" in the locomotor skills of captive *L. rosalia*. A greater frequency of small and terminal branch use by the Beaver Valley animals coupled with their higher frequencies of walking and lower frequencies of saltatory leaping may reflect their preferred means of crossing gaps in the canopy that the wild animals would cross by leaping. A greater ability, or willingness, of wild animals to cross gaps in the forest by leaping while captive animals find alternate routes is indicated by the greater frequency of leaping in wild animals and more walking in the Beaver Valley Group. Routes used by the Beaver Valley animals typically include more small and terminal supports. The data presented in Table 5 support this hypothesis. The Beaver Valley animals used branches smaller than 1.5 cm in diameter for 33% of all their walking bouts, and for 77% of all their climbing bouts. By contrast, the wild groups only used branches smaller than 1.5 cm in diameter for 14% of all walking bouts, although 66% of all climbing bouts used these supports. This may indicate that the Beaver Valley animals are walking further out into the periphery of the tree crowns than are the wild groups. In contrast, the greater reliance on larger supports in the wild groups may reflect the need for stable launching and landing platforms during leaping. Thirty-two percent of all leaping at Beaver Valley involved the smallest class of supports, as opposed to 18% at PDA. Conversely, leaping from larger supports (i.e. 1.5–12.5 cm in diameter) is more common in the wild (41% vs. 69%). We propose that the Beaver Valley animals are walking and climbing further out into the canopy before leaping to cross gaps, while the wild animals are leaping greater distances from more stable supports.

When substrates are broken down according to inclination (Figure 7), it is apparent that captive animals strongly prefer horizontal supports (Table 3). Although wild animals appear to show a slight preference for vertical supports, they also use horizontal and diagonals with similar frequency. It is interesting that under the protocols for which these data were collected, the wild animals show a greater preference for terminal supports than the Beaver Valley animals, somewhat contrary to the discussion above. This is because

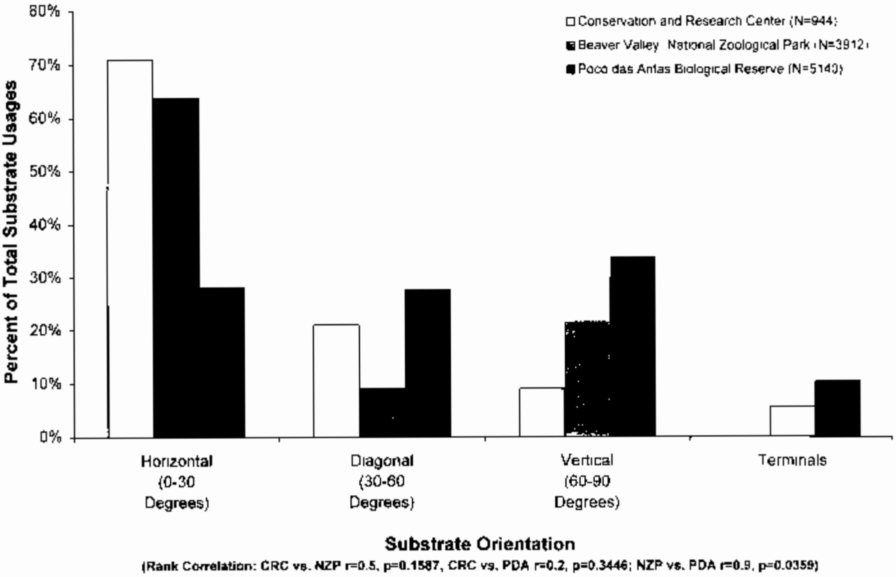


Figure 7. Substrate orientation use by *Leontopithecus rosalia*.

the category "terminals" is a structural, and not a size, category. Terminal branches are, by definition, smaller than 1.5 cm in diameter, but not all branches less than 1.5 cm in diameter are terminal branches. In order to qualify as "terminal branches" such small supports must have a geometrically complex structure. If the support that the animal is traveling on can be identified as a single support with a given orientation, then it is not classified as a terminal. Another point is that the concentrated use of large (>30 cm) tree trunks, which only occurs in Beaver Valley, contributes disproportionately to the vertical category in this group, while the wild animals spend relatively more time on smaller diameter vertical supports. Table 5 indicates that while 85% of all vertical climbing in Beaver Valley occurs on supports greater than 12.5 cm in diameter, in the wild 69% of all vertical climbing occurs on supports smaller than 1.5 cm in diameter.

Forest level usage also differs between our study groups (Figure 8). The animals at CRC were constrained by the fact that their cages were only just a little over two meters high and they will not be further discussed. The more evident similarities between the Beaver Valley and PDA groups are somewhat difficult to evaluate because the relatively greater use of the subcanopy at Beaver Valley relates to the arrangement of the ropes which were attached below the tree crowns. To what degree the Beaver Valley animals would have used the canopy in the absence of the ropes is difficult to say. We have noted (Stafford *et al.*, 1994) that the removal of two of the peripheral ropes in Beaver Valley did seem to elicit locomotion in the canopy along paths previously crossed by the ropes, but to what degree this was a result of rope removal, or increased locomotor competency in the animals is unknown (see Price, 1994 for an excellent study of *Saguinus oedipus* under similar but better controlled circumstances). In general, Beaver Valley offers a closer approximation of wild conditions in terms of the levels of the forest used.

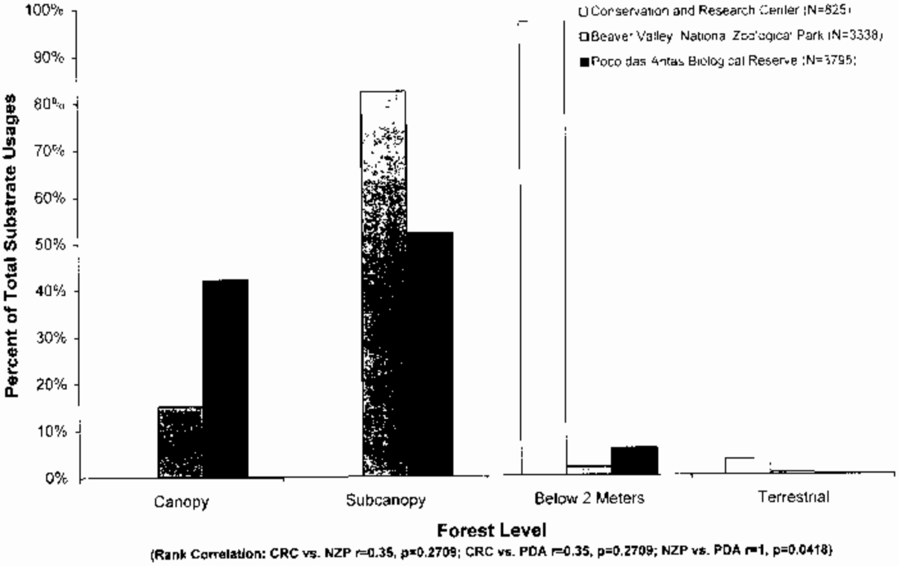


Figure 8. Use of forest level by *Leontopithecus rosalia*.

CONCLUSIONS

The results of this study lead us to several conclusions.

1. The locomotor profiles of *L. rosalia* in the wild and captivity are different. This difference appears to be manifested in a greater reliance on horizontal supports, a reduced degree of leaping-g behavior, and an increased reliance on a single form of quadrupedal locomotion in captive animals. In comparison, wild groups used leaping and vertical climbing as their primary locomotor choices, followed by variations of quadrupedalism-g.
2. The Beaver Valley environment seems to approximate the wild conditions better than the "conventional" enclosures at CRC. Even so, we would urge caution when positioning substrates into exhibits because of the apparent associations between specific locomotor categories and certain substrates.
3. The unique nature of quadrupedalism in *L. rosalia* is best explained as the result of incorporating foraging adaptations into the locomotor system, and not of locomotor adaptations *per se*. This unique pattern of cheiridial placement, now confirmed as the common pattern of *L. rosalia* in the wild, is constrained by forelimb morphology and is never seen to vary between settings.
4. The use of generalized locomotor categories to characterize the locomotor profile of any species may underrepresent the diversity of behaviors being used. Narrowly defined locomotor categories based on footfall patterns and kinematics may offer more acute insight into the specific correlations between locomotor behavior and morphology.
5. Captive studies are important because they offer opportunities to study behaviors without the obstructions present in the field. They allow experimentation, allowing the researcher to eliminate substrate as a variable between taxa, and to evaluate the effects of substrate size and inclination on locomotion.

Finally, as a general comment regarding the characterization of locomotion in *L. rosalia*, we point out that the locomotor profile of the wild animals suggests caution concerning our earlier hypothesis (Rosenberger and Stafford, 1994) which cast *L. rosalia* as a basically quadrupedal species based on our comparison with *Callimico*. In the wild, *L. rosalia* apparently use equal amounts of quadrupedalism and leaping. This makes their classification as "basically quadrupedal" somewhat problematic. A critical piece of missing information is comparative locomotor data on other callitrichines living in the same environment. Such studies could easily answer the question of whether or not *L. rosalia* are relatively more quadrupedal than other callitrichines as their morphology suggests.

SUMMARY

We report here on the locomotor behavior of three groups of golden lion tamarins (*Leontopithecus rosalia*); one in conventional captive enclosures, another in a captive free-ranging setting, and a third in the wild in Brazil. We find that *L. rosalia* appear to be more quadrupedal than other callitrichines in captivity, and that they use a unique mode of quadrupedal progression probably related to the elongate manus of this genus. We propose that the unique character of locomotion in *L. rosalia* is the result of incorporating foraging specializations into the locomotor system, rather than consider it a locomotor adaptation in the strictest sense. We found that locomotion did differ significantly between our

groups, and that there were close associations between certain substrate types and certain locomotor behaviors for all groups. We propose that the different environments between the study sites drives this difference in locomotor behavior. While the locomotor behavior of the wild groups studied was different than that of the captive groups studied, there were few differences in the locomotion between wild groups in spite of the fact that there appear to be substantial differences in utilized substrates. We propose that morphological constraints explain this relative constancy in locomotor behavior between the wild sites.

ACKNOWLEDGMENTS

For access to the animals housed at CRC we thank Chris Wemmer and Larry Collins. Kim Pojeta was always helpful, and tolerant of our presence, during this phase of the project; especially when it came time to put ink on the hands and feet of the monkeys. The hand- and footprints presented here were collected by Doug C. Broadfield, who also assisted in the early development of the CRC study and data collection. Similarly, the staff at the National Zoological Park responsible for the daily management of the animals at Beaver Valley, under the direction of Lisa Stevens, were always helpful. At Poço das Antas, special thanks go to Andrea Martins and Denise Rambaldi for solving numerous logistical problems for us over the years. We would also like to thank the members of the ecology and reintroduction teams working in Brazil. They have proved a valuable and reliable source of information on golden lion tamarins.

Financial support has been provided by the Smithsonian Institution International Environmental Sciences Program, the Smithsonian Institution Scholarly Studies Program, the National Zoological Park (Research Development Award), Friends of the National Zoo, Brookfield Zoo (The Chicago Zoological Society), World Wildlife Fund for Nature - WWF, National Geographic Society, National Science Foundation (grant # DBS9008186), TransBrasil Airlines, the Brazilian Institute of the Environment and Natural resources (IBAMA), and the Brazilian National Council for Scientific and Technological Development (CNPq).

REFERENCES

Altmann, J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–265.

Beck BB, Kleiman DG, Dietz JM, Castro I, Carvalho C, Martins A, and Rettberg-Beck B (1991) Losses and reproduction in reintroduced golden lion tamarins *Leontopithecus rosalia*. Dodo 27:50–61

Cartmill, M (1985) Climbing. Pp. 73–389 in M Hildebrand, DM Bramble, HF Liem, and DB Wake (eds.) Functional Vertebrate Morphology. The Belknap Press of Harvard University Press, Cambridge, massachusetts.

Coimbra-Filho AF, and Mittermeier RA (1978) Reintroduction and translocation of lion tamarins: a realistic appraisal. Pp. 41–46 in H Rothe, H Woters, and JP Hearn (eds.) Biology and Behavior of Marmosets. Eigenverlag Hartmut Rothe, Gottingen.

Dietz JM, Baker AJ, and Miglioretti D (1994) Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). American Journal of Primatology 34:115–132.

Dykj D (1982) Allometry of the trunk and limbs in New World Monkeys. Doctoral Dissertation, City University of New York.

Fleagle JG (1988) Primate Adaptation and Evolution. Academic Press, Inc., New York.

Ford SM (1994) Evolution of sexual dimorphism in body weight in platyrrhines. American Journal of Primatology 34:221–244.

Ford SM and Davis LC (1992) Systematics and body size: implications for feeding adaptations in New World monkeys. American Journal of Physical Anthropology 88:415–468.

Garber PA (1980) Locomotor behavior and feeding ecology of the Panamanian tamarin *Saguinus oedipus geoffroyi* (Callitrichidae, Primates). International Journal of Primatology 1:185–201.

Garber PA (1991) A comparative study of positional behavior in three species of tamarin monkeys. Primates 32:219–230

Garber PA (1992) Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. American Journal of Physical Anthropology 88:469–482.

GeboDL, and Chapman CA (1995) Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys. American Journal of Physical Anthropology 96: 73–82.

Grand, TI (1967) A mechanical interpretationof terminal branch feeding. Journal of Mammalogy 53:198-201.

Hampson, CG (1965) Locomotion and some associated morphology in the Northern flying squirrel. PhD Dissertation, University of Alberta.

Hildebrand M (1967) Symmetrical gaits of primates. American Journal of Physical Anthropology 26:119–130.

Hildebrand M (1977) Analysis of asymmetrical gaits. Journal of Mammalogy 58:131–156.

Hildebrand M (1980) The adaptive significance of tetrapod gait selection. American Zoologist 20:255–267.

Jungers WL (1977) Hindlimbs and pelvic adaptations to vertical climbing and clinging in *Megaladapis*, a giant subfossil prosimian from Madagascar. Yearbook of Physical Anthropology 20:508–524.

Kleiman DG (1989) Reintroduction of captive mammals for conservation. BioScience 39:152–161.

Kleiman DG, Beck BB, Dietz JM, Dietz LA, Ballou JD, and Coimbra-Filho AF (1986) Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies, and reintroduction. Pp. 959–979 in K Benirschke (ed) Primates the Road to Self-Sustaining Populations. Springer-Verlag, New York.

Kleiman DG, Beck BB, Dietz JM, and Dietz LA (1991) Costs of a re-introduction and criteria for success: accounting and accountability in the golden lion tamarin conservation program. Symposium of the Zoological Society of London 62:125–142.

Martin RD (1990) Primate Origins and Evolution. Princeton University Press, Princeton.

Napier JR, and Walker AC (1967) vertical clinging and leaping - a newly recognized category of locomotor behavior of primates. Folia Primatologica 6:204–219.

Peres CA (1986) Costs and benefits of terretorial defense in golden lion tamarins, *Leontopithecus rosalia*. MS Thesis, University of Florida.

Price EC (1994) Adaptation of captive-bred cotton-top tamarins (*Saguinus oedipus*) to a natural environment. Zoo Biology 11:107–120.

Prost JH (1965) A definitional system for the classification of primate locomotion. American Anthropologist 67.1198 1214.

Ripley S (1967) The leaping of langurs: a problem in the study of locomotor adaptation. American Journal of Physical Anthropology 26:149–170.

Rollinson J, and Martin RD (1981) Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. Symposium of the Zoological Society of London 48:377–427.

Rose MD (1973) Quadrupedalism in Primates. Primates 14:337–357.

Rosenberger AL (1992) Evolution of feeding niches in New World monkeys. American Journal of Physical Anthropology 88:525–562.

Rosenberger AL, and Stafford BJ (1994) Locomotion in captive *Leontopithecus* and *Callimico*: a multimedia study. American Journal of Physical Anthropology 94:379–394.

Rylands AB (1989) Sympatric callitrichids: the black tufted-ear marmoset, *Callithrix khuli*. and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. Journal of Human Evolution 18:679–695.

Rylands AB (1993) The ecology of the lion tamarins, *Leontopithecus*: some intrageneric differences and comparisons with other callitrichids. Pp. 296–313 in AB Rylands (ed.) Marmosets and Tamarins. Systematics, Behavior, and Ecology. Oxford University Press, Oxford.

Stafford BJ, Rosenberger AL, and Beck BB (1994) Locomotion of free-ranging golden lion tamarins (*Leontopithecus rosalia*) at the National Zoological Park. Zoo Biology 13:333–344.

Thorington RW, and Heaney LR (1981) Body proportions and gliding adaptations of flying squirrels (Petauristinea). Journal of Mammalogy 62:101–114.

Thorington RW, and Thorington EM (1989) Postcranial Proportions of *Microsciurus* and *Sciurillus*, the american pygmy tree squirrels. Advances in Neotropical Mammalogy 1989:125–136.

Vilensky JA (1989) Primate Quadrupedalism: how and why does it differ from that of typical quadrupeds? Brain behavior and Evolution 34:357–364.

Vilensky JA, and Larson SL (1989) Primate locomotion: utilization and control of symmetrical gaits. Annual review of Anthropology 18:17–35.