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Locomotion in Captive *Leontopithecus* and *Callimico:* A Multimedia Study

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ABSTRACT Video studies, gait analysis, footprint tracks, and observational scan sampling show that, in comparably furnished enclosures, *Leontopithecus rosalia* and *Callimico goeldii* are superficially similar in their use of predefined locomotor patterns but differ profoundly in many underlying details which reflect differences in postcranial morphology. Each uses pronograde arboreal quadrupedal walking, quadrupedal bounding, and vertical climbing with comparable frequency, and both shift to bounding while moving quadrupedally at high speeds. In walking, both species use a diagonal sequence gait. However, in *Callimico* the distance per bout traveled while walking or running is shorter than in *L. rosalia* and there is an emphasis on leaping (from a stationary position) and bounding-leaps (saltational extensions of pronograde quadrupedalism), in contrast with the basically quadrupedal style of *L. rosalia*. This dichotomy is consistent with anatomical specializations, such as forelimb elongation in *Leontopithecus* and hindlimb elongation in *Callimico*. In vivo hand- and footprint studies demonstrate grasping halluces in both species while walking. Limb stances in *L. rosalia* during "transaxial bounding" involve an overstriding hindlimb, a predominance of oblique rather than in-line travel, and unique hand and foot positions. Anatomically, this locomotor style may be associated with reduced dexterity of the elongate hands and a relatively short hallux. The captive locomotor profiles for both species probably reflect biased samples of the locomotor repertoire of their wild counterparts. Nevertheless, these data reflect species-specific integrations of locomotor behavior and morphology, and corroborate expectations of locomotor diversity among callitrichine primates, even those of similar body size. It is suggested, however, that conventional quantitative studies of locomotor profiles may prove inadequate for resolving subtle aspects of locomotor morphology and behavior.

Basic data on the positional behavior (Prost, 1965) of callitrichine primates are extremely rare. The most detailed information comes from Garber (1980, 1984, 1991), who studied the interrelationships between positional behavior, substrate use, feeding ecology and traveling patterns in *Saguinus,* particularly the Panamanian Tamarin, *S. oedipus geoffroyi.* Far less is known about other species (Garber, 1992). Consequently, any links between morphology and positional behavior in callitrichines are tenuous, in spite of a considerable interest in their postcranial anatomy (e.g., Ford, 1988, 1990; Gebo, 1989).

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In this report, we discuss the locomotor behavior of captive golden lion tamarins, *Leontopithecus rosalia,* and Goeldi's monkeys, *Callimico goeldii.* We gathered several types of information and employed a number of approaches. These included direct scan sampling of locomotor bouts, behavioral sampling of videotapes, slow-motion playbacks of locomotor sequences from videotape, gait analysis, and footprint studies of stance and limb positions during quadrupedal locomotion.

MATERIALS AND METHODS

Subjects and enclosures

Our subjects were four *Leontopithecus rosalia* and 14 *Callimico goeldii,* all nonbreeding adults, living in six adjacent outdoor enclosures at the Conservation Research Center in Front Royal, VA, an affiliate of the National Zoological Park/Smithsonian Institution. Most of the *Callimico* were kept in groups of two to six individuals, but two were housed with lone *L. rosalia* in separate enclosures. Two *L. rosalia* were kept together in their own cage. All animals were well habituated to people, but given additional time to adjust to the observers before we collected data or ran tests. Observations and trials were conducted July–October 1991, between 08:00 and 17:00 hr.

Each enclosure measured 24 feet long × 12 feet wide × 8 feet high. They were divided from one another by cinder block walls, faced and roofed over by conventional wire mesh (cyclone) fencing, and furnished with a central, rectangular "arboreal" framework of stable supports made of firmly connected dead falls, 4–20 cm in diameter, collected from the neighboring forest. The branches were set 5–7 feet above the concrete floor. Other supports, most about 4 cm in diameter or slightly narrower, provided additional access to the corners, walls, roof, and floor. These were of moderate size relative to the size of the monkeys, whose feet are 7–8 cm in length and whose head-and-body lengths average 229 mm in *L. rosalia* and 225 in *C. goeldii* (Hershkovitz, 1977). The entire network was arranged in a predominantly horizontal (<30°) fashion but some enclosures did contain a relatively thick upright trunk or narrow vines or ropes, usually one or two per cage, strung to provide inclined (between 30° and 60°) routes.

Definitions and recording techniques

A locomotor bout (Fleagle and Mittermeier, 1980; Gebo, 1987) was defined in terms of four concurrent behaviors or elements: (1) a discrete uninterrupted movement covering a distance of 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 below, and (4) absence of postural interruptions lasting more than approximately 3 sec. Thus displacements that chained together locomotor styles sequentially, as in the series walk–leap–walk, were regarded as three bouts. Events which spanned two types of supports, or were punctuated by pauses greater than 3 sec, were scored as multiple bouts. Seven locomotor categories were scored:

1. Quadrupedal walking. No distinction was made between walking and running, which tended to involve continuous quadrupedal locomotion using a regular gait sequence such as the diagonal couplets pattern (see Hildebrand, 1967), and appeared to differ only in velocity.

2. Quadrupedal bounding. Hildebrand (1967), in a paper concerned largely with footfall configuration, defined bounding as "an asymmetrical gait having the footfalls of one or both pairs of feet unevenly spaced in time" (p. 119). Bounding, as used here and in various related papers (Gebo, 1987; Garber, 1984; Fleagle and Mittermier, 1980), is applied in a broader sense to distinguish it from quadrupedal walking. It is a form of pronograde quadrupedalism distinguished by strong hindlimb propulsion, a tendency towards an in-air phase, a syncopated limb cadence, and exaggerated hindlimb thrusting. The bound of *L. rosalia* resembles a "transverse gallop" while the bound of *Callimico* is a "half bound" (see Hildebrand, 1989 for definitions).

3. Leaping. Saltation from a stationary posture.

4. Bounding-leap. Airborne extensions of arboreal quadrupedal walking or bounding used, for example, when crossing between supports or traversing bends or obstructions along a support.

5. Vertical climbing. Ascent of a steeply inclined (>60°) support using a near-orthograde quadrupedalism (including vertical bounding).

6. Suspension. Walking suspended below a support, using all fours.

7. Terrestrial. Pronograde locomotion on the cage floor.

It should be noted that the substrate arrangements of the enclosures were not conducive to vertical clinging and leaping, which plays a vital role in the normal repertoire of at least some feral callitrichine species (Kinzey et al., 1975; Garber, 1980, 1984, 1991, 1992). "Gap bridging" and "arboreal quadrumanous climbing" were also observed and recorded but are not included in the final analysis. Neither behavior was seen in *Callimico*, and the latter occurred at a frequency of less than 1% in *L. rosalia.*

To obtain frequency distributions of locomotor behavior, locomotor bouts were recorded using two approaches, by conventional scan sampling and from videotape. Data collected by direct observation were immediately entered on a checksheet listing all of the behavioral categories. Substrate was also registered as it related to delineation of behaviors and bouts. The same procedures were followed in obtaining data from videotapes which were replayed on a video cassette recorder. In both cases locomotion was sampled on an ad libitum basis to take advantage of the animals' natural activity rhythms and avoid bias toward any particular cage or set of individuals. Periodically, we switched between cages in order to collect as much movement data as possible. Unless specified otherwise, the two sampling methods were not employed simultaneously on the same animal(s). Data collected by direct observation were collected by one observer, and much of the videotape data was evaluated by both of us.

For video recording, we used a high-resolution 8-mm (Hi-8) digital camcorder, fixed with a 210-mm telephoto lens and mounted on a fluid-head tripod. Recording speed was 30 frames per second and a variety of shutter speeds were employed, generally 1/100 to 1/1,000 of a second. To play back videotape, we used a Hi-8 tape deck with freeze-frame capability and a jog shuttle dial. The latter enabled us to locate study sequences precisely, control the rate at which video was replayed, and observe the images in forward and reverse modes. Playbacks were studied on a high resolution video monitor. Gait sequences retrieved from video were diagrammed following the methodology of Hildebrand (1967). This involves charting the footfall events of a step cycle as they occur sequentially in individual video frames. According to convention, we defined the step cycle as the period between successive contacts of the left hindlimb. Spread length refers to the greatest distance between the points of "heelstrike" of either ipsilateral or contralateral footprints made during the stance phase of the step cycle.

Hand and foot prints

To study the manner in which hands and feet were oriented on arboreal supports, we obtained inked tracings of the cheiridia as animals moved on a relatively horizontal (<30°), smooth wooden dowel, approximately 2 m long and 3.2 cm in diameter. The dowel was wrapped tightly with a strip of blank newsprint fixed with masking tape. A centerline was marked on the upper surface with a snapline to verify orientation and reference the spatial relationships of anatomical features. Commercially available fingerprint ink was applied over an area at one end of the dowel for approximately 30 cm. During trials, an animal was enticed onto the ink by offering a raisin. When the hands and feet seemed adequately coated, the subject with offered another raisin at the other end of the dowel. In all cases, the mode of locomotion was self-determined by the animal rather than elicited by the observer. When possible, we confirmed the style of locomotion by reviewing videotapes. The animals seemed unaware or uninterested in the ink, and there was no evident interference with their behavior. For each traverse, this

TABLE 1. Comparison of observed and filmed locomotor bouts in Leontopithecus rosalia *and* Callimico goeldii

	AQW	AQB	L	BL	VCb	Su	T	Number of bouts
L. rosalia								
Observed								
Cage #4[1]	8	16	17	4	5	10	0	60
Cage #1[2]	11	26	22	4	11	3	2	79
	14%	30%	28%	6%	12%	9%	1%	
Filmed								
Cage #4	5	14	5	7	6	7	0	44
Cage #1	9	26	20	20	4	3	2	84
	11%	31%	24%	24%	5%	4%	2%	
Callimico								
Observed								
Cage #5[3]	2	34	3	14	6	0	0	59
Cage #1	0	7	7	1	1	0	0	16
	3%	55%	13%	20%	9%	0%	0%	
Filmed								
Cage #5	1	31	21	15	11	0	0	79
Cage #1	0	27	18	20	1	0	0	66
	1%	40%	27%	24%	8%	0%	0%	

[1] Cage #4 contained two *L. rosalia*.
[2] Cage #1 contained one *L. rosalia* and one *Callimico*.
[3] Cage #5 contained two *Callimico*.

technique produced a set of prints for one or two complete strides.

RESULTS

Video as an input device

As we chose to implement a video-based approach, we were interested in evaluating this technology for data capture. Thus we contrived a test to compare the quality and quantity of locomotor data obtained by direct observation as opposed to video. Three enclosures were studied during a 1.5 hr session with 0.5 hr devoted to each cage. One enclosure contained two *L. rosalia*, one had two *Callimico* and one a mixed-species pair. Bouts were recorded directly by one observer while another videotaped the animals in the same cage. The objective of each worker was to obtain as much locomotor data as possible, and there was no effort to coordinate scoring or recording of a specific animal at a given moment. Bout data were later gathered from the videotape by the same person who had scored behavior visually. Although the tape would occasionally include more than one animal moving within a cage, only 1% of the samples included data for multiple subjects.

As expected, video produced more bouts than visual scanning (Table 1). During our study period, 214 bouts of locomotion were recorded through visual scanning and 273 were registered from the video. This resulted in an hourly rate of 143 records collected by eye and 182 via video. These figures are comparable to the normal averages established during the course of our study. Generally, we found that over a 5- or 6-hr session, visual scanning yielded about 100 bouts per hour while video generated about 200 bouts per hour.

A detailed examination of the distribution of behaviors within and between species (Table 1, Fig. 1a and b) indicates that there are important qualitative differences between the data collected in each medium. Some discrepancies between visual- and video-based data relate to species-specific locomotor patterns. For example, the eyeball method appears to underrepresent the number of locomotor events, in part because the animals continue to locomote while the observer enters data. For *Callimico,* nearly twice as many bouts were recorded on video as on the checksheet. For *L. rosalia,* on the other hand, there was only a 9% discrepancy favoring video, possibly reflecting the slower, less saltatory character of their locomotion, a pattern apparently less prone to classification errors.

In *Callimico* the discrepancies associated with quadrupedal bounding, leaping, and bounding-leaps may also be linked (Fig. 1b). We surmise that these categories, which

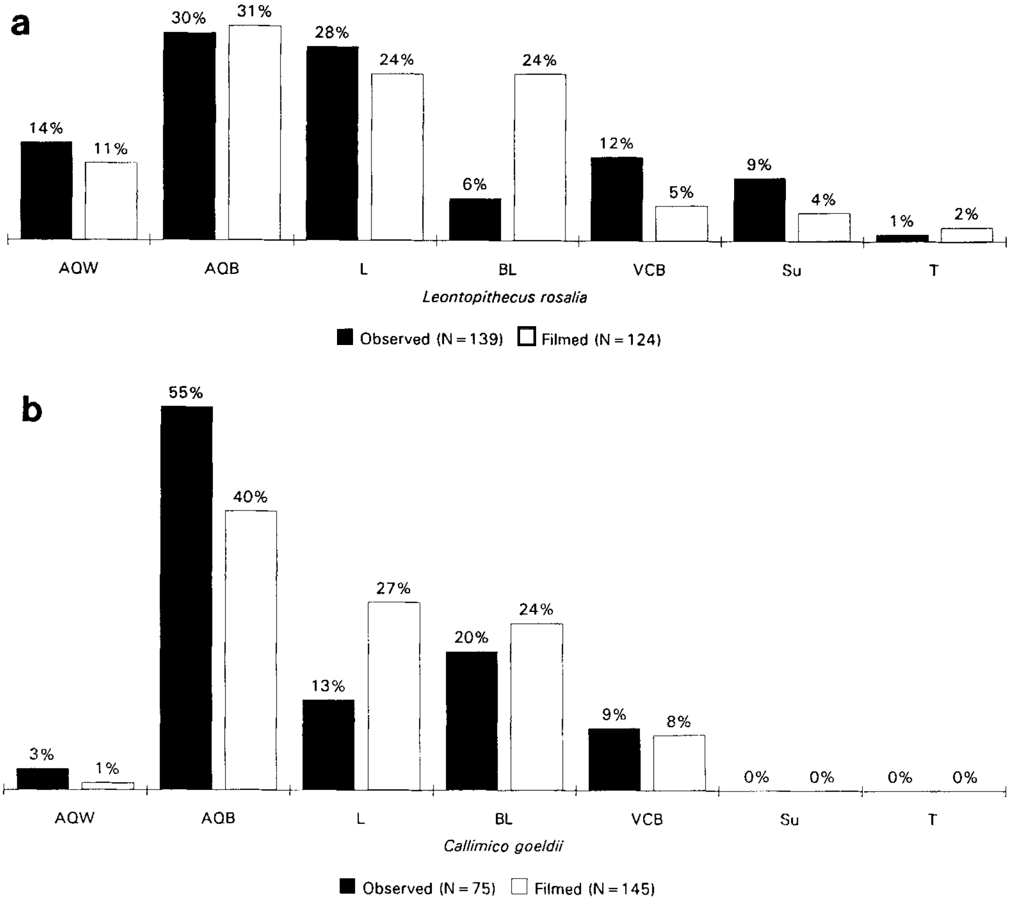


Fig. 1. Comparison of observed and filmed locomotor profiles of *L. rosalia* (a) and *C. goeldii* (b). AQW, arboreal quadrupedal walking; AQB, arboreal quadrupedal bounding; L, leaping; BL, bounding-leaping; VCB, vertical climbing; Su, suspension; T, terrestrial quadrupedalism.

may grade into one another, are prone to scoring error when the animals are making long, rapid traverses away from the observer, as when moving from the front of a cage to the back. Events that may have been scored as a single bout of arboreal quadrupedal bounding may, in fact, have represented a sequence of bounding and bounding-leaps chained together. Finally, for both species, leaping was a surprising source of coding error. This may reflect methodological difficulties, since leaping is the only locomotor category whose definition requires that the observer verifies the starting condition, which is the absence of movement, as well as the terminal substrate. Thus, in general, video produced more bouts overall and made it possible to verify subtleties in locomotor style too elusive for the naked eye to see. Data from both media were combined for the overall analysis as they appear to be complimentary, each with their own strengths and weaknesses.

Locomotor behavior

Figure 2 presents comprehensive profiles of the locomotor behavior of *L. rosalia* and *Callimico* compiled from bout records using video and direct scanning (65 and 54% of total records, respectively). Data were collected on six separate days during three sampling periods, one early in July, a second late in July, and the third in early October. The number of bouts recorded per day

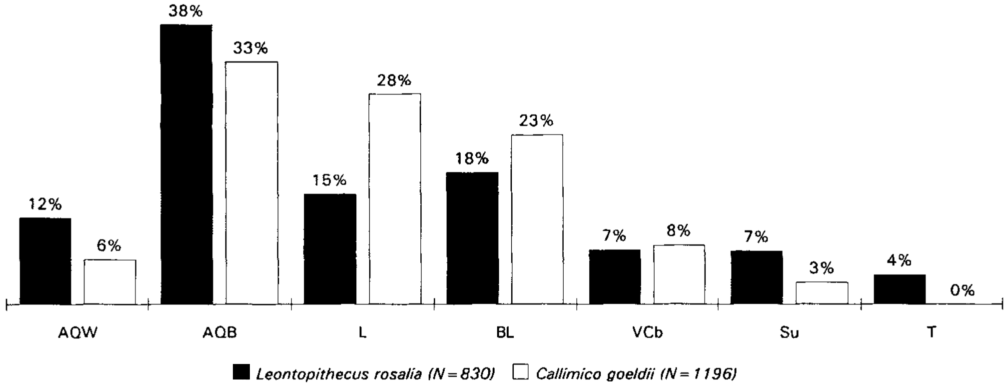


Fig. 2. Locomotor profiles of *L. rosalia* and *C. goeldii*. See Figure 1 for conventions.

TABLE 2. Frequencies of locomotor behaviors (percentages of total bouts) in Leontopithecus rosalia *(LR) and* Callimico goeldii *(CG): visual observation, video observation, and combined data*

	Quadrupedal		Leaping		Vertical climbing		Suspension	
	LR	CG	LR	CG	LR	CG	LR	CG
Visual	50	37	30	47	8	9	9	5
Video	48	41	34	52	11	7	6	2
Combined	50	39	33	51	7	8	7	3

ranged from 73 to 368. Data obtained from video and from direct visual observation revealed essentially identical patterns of interspecific similarities and differences (Table 2) and so the two data sets are combined in the following analysis. In all, *Callimico* is represented by 1196 bouts and *L. rosalia* by 830.

Arboreal quadrupedal walking, bounding, leaping, and bounding-leaps were the predominant modes of locomotion for both species, accounting for over 75% of all bouts. Terrestrial quadrupedal walking, vertical climbing, and suspension were used to lesser degrees. Quadrumanous climbing and gap bridging were rarely employed. *L. rosalia* shows a dramatically lower incidence of leaping and bounding-leaps and these two categories distinguish the species to the greatest degree. Therefore, we interpret *L. rosalia* as a basically arboreal quadruped and *Callimico* as a leaper. This is shown most dramatically by the lower cumulative incidence of leaping plus bounding-leaps in *L. rosalia* (33%), vs. *Callimico* (51%). This generalization is further indicated by more subtle differences, such as the relatively higher frequency of walking (12 vs. 6%), and suspensory behavior (7 vs. 2%) in *L. rosalia* (Fig. 2).

Although they were rare events, vertical climbing and suspension were used with equal frequencies in *L. rosalia*, in contrast to a ratio of 4:1 in *Callimico*. *L. rosalia* tended to use the cage-wire ceiling more frequently, walking quadrupedally upside down to cross open areas in the cage. *Callimico* rarely if ever suspended from or walked quadrupedally below the ceiling mesh. They tended to cross gaps in the cage by leaping.

The importance of leaping in *Callimico* was evident in several other ways. *Callimico* jumped from a stationary position much more often than *L. rosalia* (28 vs. 15%), even when they were housed in the same enclosures. Leaping and bounding-leaps accounted for 51% of all bouts in *Callimico*. They tended to cross between supports or pass bends or obstructions using these patterns, whereas *L. rosalia* tended to plot continuous quadrupedal routes. Futhermore, they used arboreal quadrupedalism more of-

TABLE 3. Support and contact combinations in L. rosalia *and* C. goeldii

	Number of sequences	Average number of frames per sequence	Average limb contacts with substrate[1] (%)					Hindlimb–forelimb contact combinations[2] (%)		
			0	1	2	3	4	H–H	H–F	F–F
L. rosalia										
Walk	3	12.6	0	0	56	37	7	2	98	0
Bound	5	10.5	3	13	68	14	1	29	31	24
C. goeldii										
Walk	2	9.5	0	5	40	50	0	11	74	11
Bound	5	8.5	4	15	61	12	3	41	19	25

[1] Percent of sequence that a given number of cheiridia are in contact with the substrate.

[2] Percent of sequence that a given combination of cheiridia are in contact with the substrate. H–H, hindlimb–hindlimb; H–F, hindlimb–forelimb; F–F, forelimb–forelimb.

ten than leaping (49 vs. 33%), whereas in *Callimico* leaping was used more (51 vs. 39%).

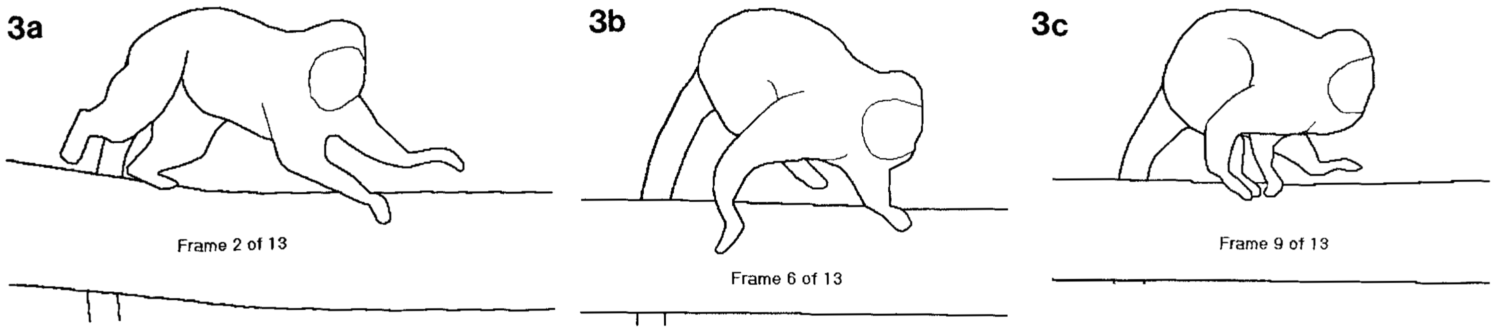
The limited contribution of quadrupedal walking to the locomotor repertoire of *Callimico* (6%) was confirmed by a detailed study of the video regarding the character of walking. This typically occurs as a short burst of behavior covering a very short distance, usually little more than a body length, involving a single stride or short, repetitive sequence of steps. Long distance moves almost always involve quadrupedal bounding or leaping. In contrast, in *L. rosalia,* walking is implemented for both long and short distances, while bounding appears to be related to a rapid rate of travel, or to negotiating obstructions or directional changes.

Gait

Fifteen complete gait sequences, ranging from one to three full step cycles and representing several individuals of each species, were selected for detailed analysis (Table 3). For quadrupedal walking and running, there were no remarkable differences between the species, although the rate of travel was faster in *Callimico* than *L. rosalia* (Table 3). Both species used a symmetrical, diagonal-sequence pattern, with the forefoot striking the support after the hindfoot of the opposite side (Figs. 3,4). Thus, synchronous contacts of feet and hands together accounted for 74–98% of cycle time (as measured in video frames), with three cheiridia in simultaneous contact 37–50% of the time. In contrast, bounding in both species involved limited hindlimb–forelimb contacts, amounting to 19–31% of cycle time, and contact triads averaging only 12–14% of cycle time. In general, the walking pattern is highly stereotyped in *L. rosalia.* Only 2% of cycle time exclusively involves the hind feet and the hands are never exclusively paired.

In contrast to *L. rosalia*, walking in *Callimico* (Fig. 7), while maintaining a diagonal sequence pattern, frequently involves a period when only the two hindlimbs or two forelimbs are in contact with the substrate, thus resembling a "half-bound" (Daag, 1973; Hildebrand, 1989). Thus, 22% of video frames (Table 3) showed synchronous stances of either the fore- or hindlimb (11% F–F; 11% H–H).

More marked differences between the species were apparent in bounding (Table 3; Figs. 3,4). For 66% of each bounding cycle, *Callimico* used either a forelimb or a hindlimb stance exclusively. Only 19% of cycle time involved fore- and hindlimb combinations. Limb pairings predominated (61%) over single (15%) or triple-limb supports (12%). The hindlimbs were paired exclusively during 41% of cycle time, whereas the forelimbs were coupled 25% of the time. Thus, kinematically, *Callimico* conforms to the weasel-like bounding discussed by Hildebrand (1989:772) in which "the hind feet strike the ground approximately in unison and the forefeet do likewise." Also, like those of other bounding mammals, the spinal column flexes deeply to bring the feet under the pectoral girdle as close to the hands as possible at push-off. It later hyperextends as the limbs are extended, producing an in-air phase between strides. Overall,



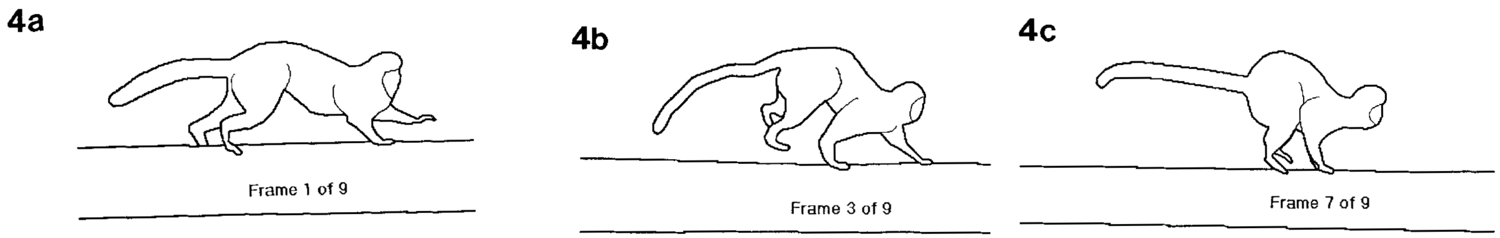


Fig. 3. (a–c) Transaxial bounding in *L. rosalia* on a horizontal branch greater than 12.5 cm in diameter, from digitized images of a typical sequence totaling 13 frames.

Fig. 4. (a–c) Bounding in *Callimico*, from a 9 frame sequence produced as in Figure 3.

these actions involve an exaggerated elevation of the entire body.

When *L. rosalia* bound, hindlimb stances amount to 29% of cycle time as opposed to 41% in *Callimico*. *L. rosalia* employ fore- and hindlimb contact combinations in roughly equal proportions (24 and 29%), resulting in a more quadrumanous variant of bounding rather than the distinctive hindlimb dominated pattern seen in *Callimico*. Bounding in *L. rosalia* differs in other aspects as well, including a longer step length between limb contacts; less dramatic extensions of the vertebral column; a shorter, more variable, free-floating phase; forelimb strikes with a more evident lead (with one forelimb advanced in front of the other, Fig. 3); and a unique orientation of the hands and feet, which we describe here as "transaxial bounding."

The defining features of transaxial bounding combine a specific pattern of limb excursions and cheridial positions. The legs of bounding *L. rosalia* typically "overstride" the forelimbs (Fig. 3b,c). That is, during protraction the foot is advanced ahead of the trailing hand to meet the substrate. The location of footstrike may be medial or lateral to the ipsilateral hand, depending if the cycle is a right- or left-sided bound, and if a side-change transition is occurring. For example, Figure 3 shows a right-sided transaxial bound. The hands are arranged on the right side of the support. The right foot swings medially to and in front of the right forelimb as it protracts and the left foot swings by the left forelimb laterally, also striking well ahead of the right hand. This overstriding reach of the hindlimbs produces an accentuated, irregular cadence to the gait, marked by strong elevations and swaying of the hindquarters. Thus, the animal progresses along a branch with all four cheiridia oriented to one side or another of the substrate during movement, occasionally swithching sides between strides.

The parallel "transaxial" arrangement of cheiridia is also evident in Figure 3. The right hand, for example, is strongly deviated laterally and aligned obliquely relative to the support. The right foot is also markedly deviated. Both hands and feet appear to flex around the branch rather than deploying a hallucal or pollical grasp.

Figure 5 is a posterior view of a right-sided transaxial bound up a shallow incline. The animal begins the sequence with hands, feet, and head oriented to the left and switches to the right in mid-stride, using a valuting pivot (Fig. 5e) over the strongly deviated right hand. This bout ended in a sit, with hindfeet also aligned to the right, but could equally have continued in the same form by transaxially bounding up the right fork of the support (hidden), as we observed on numerous occasions.

Cheiridial use

The inked tracks (Figs. 6,7) reveal additional interspecific differences in patterns of hand and foot placements during horizontal locomotion on a 3.2-cm dowel. For *L. rosalia* we collected 19 tracks of arboreal quadrupedal walking and transaxial bounding, and 21 tracks (16 of walking and 5 of bounding) for *Callimico*. The definition of these tracks is variable, but taken as a whole (with the analysis of videotapes made during these trials), they show that the two species differ significantly in cheiridial use. *L. rosalia* grasp the support less frequently and less powerfully, and with a generally less divergent hallux and pollex than *Callimico*. Neither species shows consistent evidence of claw use during horizontal locomotion, either in the form of an imprint or as a penetration mark.

During quadrupedal walking (Fig. 6b), *Callimico* tends to place the ipsilateral hands and feet close to one another. The cheiridia are applied near the central axis of the dowel, with the foot positioned just behind the hand. The stance of the foot is consistently twisted outward, permitting all five digits to embrace the dowel. The planta are at about 45° to the direction of travel, while the major axis of the hand may lie parallel or oblique to the line of travel. The prints of the palmar heel frequently overlap the plantar thenar pad in the area between the hallux and digit II. Both the hallux and pollex are spread away from the other digits, resting essentially at right angles to the long axes of the sole and palm. Their terminal pads reach over the centerline of the dowel axis, frequently leaving inked traces. This implies at least passive pollical and hallucial grasping for *Callimico*. In this example

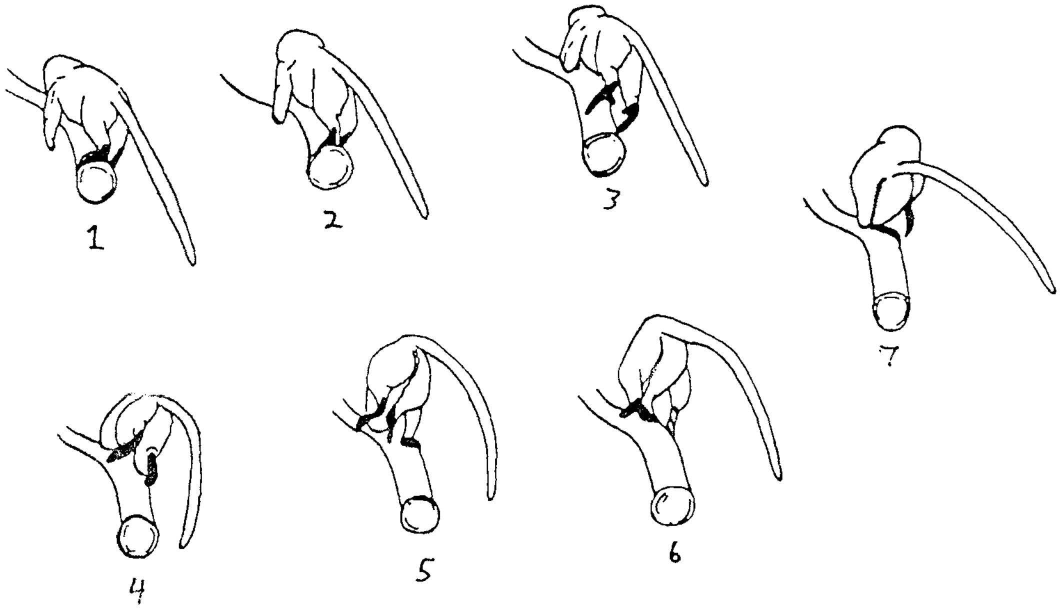


Fig. 5. A rump-view of *L. rosalia* transaxial bounding up an incline, based on frozen frames of a video sequence.

(Fig. 6b), the prints for digits II–IV are less clear than those for digit I, and mostly show terminal pad rather than interphalangeal contacts.

During quadrupedal bounding, *Callimico* positions the hands and feet differently (Fig. 7b). Step length between the limbs is short and the cheiridia are collected together under the body. However, we have found no evidence of overprints between the ipsilateral hands and feet. Frequently, right and left feet are paired adjacently about the dowel's axis with hypothenar surfaces nearly touching and the hallucial apical pads contiguous or overlapping. Hand positions, however, tend to be more irregular. The finger and toe impressions may be better preserved in bounding, indicating either greater force transmitted to the substrate, or a more powerful grasp.

For *Callimico*, the overall positioning of the cheiridia seems to be consistent with their role as a frictional base of support arranged so that the plantar and palmar dermatoglyphics would tend to resist slippage. The close spacing of hands and feet across the top and sides of the dowel and the evenness of the inkmarks (Figs. 6b,7b) suggest a shared distribution of the body's weight, with propulsive thrust transmitted advantageously close to the midline of the dowel, which is also the direction of travel. The original prints show that on the foot, the anatomical bend in the thenar pads effect an array of friction lines at right angles to the direction of progression and another at about 45° to it, and normal to the metatarsophalangeal axis. Dermatoglyphics of the hypothenar and thenar pads tend to parallel one another and lie approximately normal to axis of the hallux and its terminal glyphs. These surfaces would stabilize the foot against skidding laterally on the substrate.

In *L. rosalia*, there was more variability in stance and the overall pattern is quite unlike *Callimico*. In both walking and transaxial bounding, the ipsilateral hands and feet tended to be spaced farther apart and the four cheiridia were consistently aligned in an asymmetrical fashion (Figs. 6a,7a). Importantly, the narrow hands of *L. rosalia* were uniformly planted lateral to the dowel's central axis during both forms of locomotion. Less constant was the placement of the feet. They took up a typical hallucial grasp (Fig. 6a, right foot), a nongrasping trans-

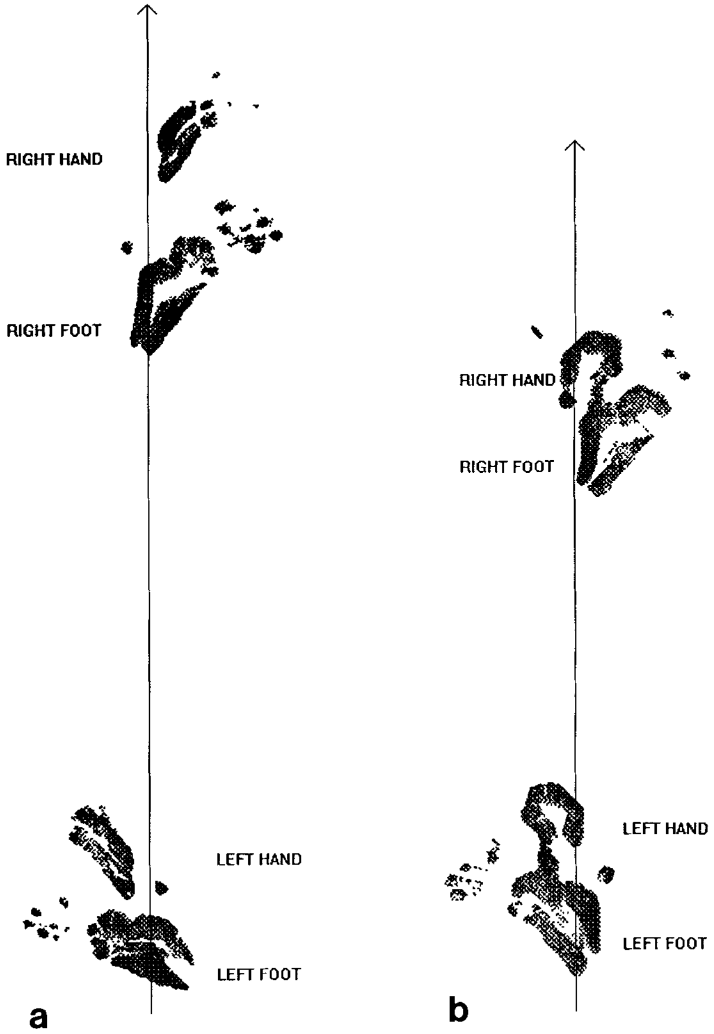


Fig. 6. Digitized hand- and footprints of *L. rosalia* (a) and *C. goeldii* (b) during arboreal quadrupedal walking on a 3.2-cm dowel. The solid line indicates centerline of the dowel. Size of prints and step length maintain the original proportions of the inked tracings.

verse plantar stance with hallux spread (Fig. 6a, left foot) and a nonhallucial flexion grasp (Fig. 7a, right foot). Additionally, we found no evidence that the pollex or fingers could be spread divergently. There were no cases where the pollex was posted across the centerline of the dowel, and few inked impressions of manual phalanges. The video corroborated this, showing that the fingers normally were flexed or curled gently along their length, as if passively draped over the support rather than clasping or gripping it. While the hallux is clearly capable of maintaining a divergent posture in spite of its relative shortness (Herskovitz, 1977), it typically did not during transaxial bounding.

Figure 7a illustrates a left-sided sequence typical of transaxial bounding in *L. rosalia*. As with *Callimico*, step length is shorter than in walking. The hands and feet appear to lie closer to the centerline of the dowel than in walking, in a flexion-type grasp. The soles of both feet are strongly deviated and arranged obliquely across the axis of the

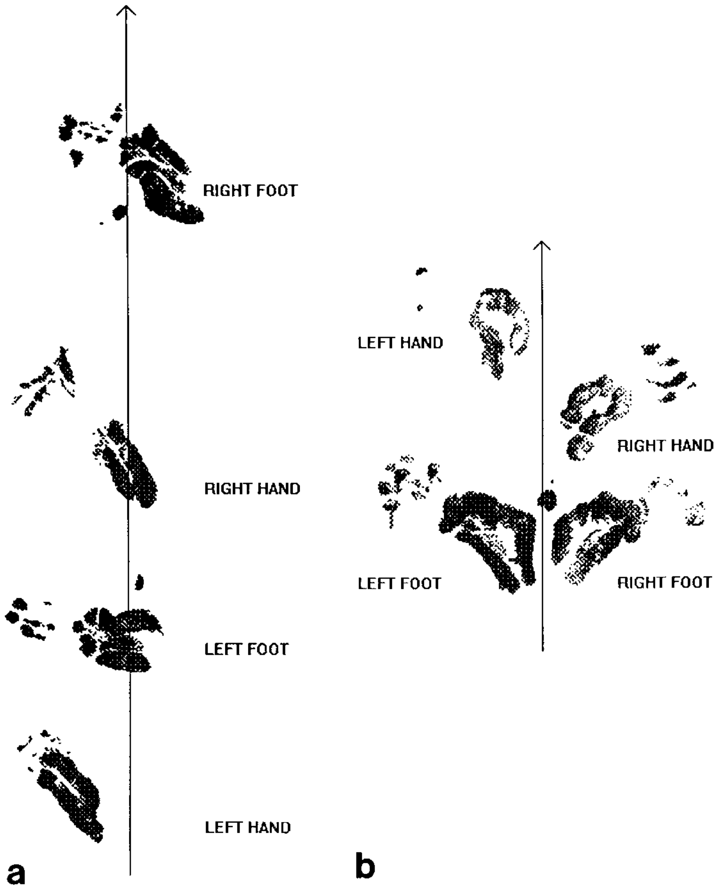


Fig. 7. Digitized hand- and footprints of (a) *L. rosalia* transaxial bonding and (b) *C. goeldii* bounding on a 3.2-cm dowel. See Figure 6 for conventions.

support. The right foot (top of figure) overstrides the laterally deviated right hand and twists inward to flex around the support, thereby precluding a hallucial grasp.

DISCUSSION

The patterns we found bear on interspecific differences in locomotor potential and reflect underlying anatomical differences between the two species. The postcranial anatomy of *Leontopithecus* and *Callimico* is not well known (Hill, 1957, 1959; Hershkovitz, 1977) and information on their positional behavior is scarce (Kleiman et al., 1988; Heltne et al., 1981). We therefore stress caution in extrapolating from our captive observations to the wild, or in developing higher-order evolutionary explanations. The impact of caging on the locomotor profiles of primates is not yet understood. Also, we regard the substrate conditions in our enclosures as nonconducive to vertical clinging and leaping, or arboreal quadrumanous climbing. Thus whole segments of the positional repertoire that may be important for callitrichines in the wild (e.g., Kinzey et al., 1975; Garber, 1980; Sussman and Kinzey, 1984) may have been artificially eliminated. Additionally, the regularity of arboreal supports and the spatial constraints of captivity may bias the development and expression of locomotion in captive animals.

Our chief findings are that *L. rosalia* and *Callimico*, in spite of their similarities in body size, tend to employ different modes of locomotion, even when housed in the same enclosures, and differ profoundly in the support functions of the hands and feet. At the risk of oversimplifying, we conclude that *L. rosalia* are quadrupedal and *Callimico* is a leaper. This confirms Garber's (1980, 1984, 1991, 1992) work, which has emphasized the diversity of callitrichine positional behavior. We further conclude that generalizations of callitrichine locomotor behavior as "scansorial" and "squirrel-like," underrepresent the diversity and complexity of these behaviors.

The limited morphological information that does exist fits well with some of our broader observations. Within the adaptive radiation of platyrrhines, characterized by a 100-fold disparity in body mass (Rosenberger, 1992; Ford and Davis, 1992), *Leontopithecus rosalia* and *Callimico goeldii* are roughly similar in mean size at 255 vs. 220 mm in head-and-body length (Herskovitz, 1977; Rosenberger and Coimbra-Filho, 1984; Lorenz and Heinemann, 1967) A recent survey of captive body weights (B. Beck, personal communication) indicates an average of 665 g for *L. rosalia* and 582 g for *Callimico*. As expected (Fleagle, 1988), captive *L. rosalia* and *Callimico* tend to employ variations of bounding and leaping as the core elements of their locomotor repertoire.

The two taxa differ in limb proportions and cheiridial morphology, and may differ correspondingly in behavior. For both species, quadrupedal bounding is the predominant mode of locomotion, with bounding, leaping, and bounding-leaps accounting for a majority of bouts; 70% in *L. rosalia* and 84% in *Callimico*. However, by comparison with *L. rosalia*, the proportion of leaping in *Callimico* is much higher.

Leontopithecus have relatively long forelimbs and *Callimico* have relatively long hindlimbs. Relative to body weight (Dykyj, 1982), *Leontopithecus* have a long humerus, radius and metacarpal III, whereas *Callimico* have long femurs, tibiae, and metatarsal III. The skeletal indices presented by Dykyj (Table 4) confirm this contrast. Additionally, Jungers (1985) has shown that, within the lower limb, the tibia of *Leontopithecus* is long relative to the femur.

TABLE 4. Limb indices in L. rosalia *and* C. goeldii

	Leontopithecus rosalia	*Callimico goeldii*
Intermembral index	88	71
Forelimb index[1]	72	64
Hindlimb index[2]	82	90

[1] (Humerus + radius)/skeletal trunk length.
[2] (Femur + tibia)/skeletal trunk length.

The correlation of long hindlimbs with leaping in primates, irrespective of phylogenetic affinity, is well established (e.g., Napier and Napier, 1967; Fleagle, 1988; Strasser, 1992). This is consistent with the emphasis on leaping in *Callimico*, as opposed to the quadrupedalism of *L. rosalia*, which is consistent with their proportionately shorter hindlimbs. The higher intermembral index, which is nearer to unity in *L. rosalia* than in other callitrichines (cf. Jungers, 1985), corresponds to greater frequencies of quadrupedal walking and bounding. Finally, within the hindlimb, the relatively long tibia of *L. rosalia* may relate to the overstriding gait that predominates during transaxial bounding, the objective of which, like other bounding gaits, is to increase stride length. A relatively long tibia (hip flexion notwithstanding) may contribute to this by exaggerating the exercusive arc of the most distal points of the lower limb, while also increasing the velocity of excursion.

Differences in limb proportions and cheiridial morphology may subtly influence gait in the two species. The broad similarities in quadrupedal walking are probably best explained as retentions of the diagonal-sequence pattern, which is typical of most primates (Hildebrand, 1967; Rollinson and Martin, 1981; Vilensky and Larson, 1990). However, while *L. rosalia* adopt a typical diagonal couplets pattern in walking, *Callimico* walks tend to resemble the half-bound described by Dagg (1973) and Hildebrand (1989), where forelimbs and hindlimbs act nearly synchronously and take up a gathered position during the support and propulsive phases of the step cycle.

During more rapid travel, however, these species enlist different gaits. *Callimico* utilize a typical mammalian half-bound while *L. rosalia* employ a transverse gallop. Even more, their hindlimb excursion patterns, and especially their hand and foot arrangements, are radically different. The transaxial bounding of *L. rosalia* incorporates a marked overstriding gait, reminiscent of chimpanzees and orangutans (Hildebrand, 1967), wherein a foot is advanced in front of the ipsilateral hand. In *L. rosalia*, as in the apes, who also possess elongate forelimbs, this is accompanied by a sideways yawing of the trunk in the line of travel, and shifts between a right- and left-side lead over the course of several strides. In contrast, the "weasel-like" bounding of *Callimico* is much less complex dynamically, without overstriding, evident yawing of the body or pro forma side switches.

Bounding in *L. rosalia* and *Callimico* also appears to differ kinematically. *Callimico* seem to employ a conventional pattern (Fig. 4), using axial flexion of the vertebral column to gather the limbs beneath the body (Fig. 7b). In *L. rosalia*, during transaxial bounding, there is an accentuated lateral deviation of the rump in order to orient the pelvis and enable the hindlimbs to overstride the forelimbs (Figs. 3c, 5, 7a).

The complex hand and foot positions taken up during transaxial bounding in *L. rosalia* are a remarkable feature of their locomotor repertoire, and may be related to their uniquely elongated forearms and hands. What is perhaps most striking about this pattern is the lack of integrated pedal grasping. Using what the human observer might interpret as an awkward stance, *L. rosalia* rotate the hindlimb medially as they make contact. The feet are set atop the support to apply a flexion grasp across the branch instead of being placed laterally alongside the branch to make a hallucial grasp possible (Fig. 7a).

We further suspect that the stances employed by *L. rosalia* during transaxial bounding reflect a diminished or altered functionality of the hands and feet, specifically in their grasping ability. They probably lack the capacity to grasp with the pollex. Yet we were surprised to find that the long, slender hands are normally placed in a manner that precludes conventional flexion grips using the palm and fingers. One may expect that during transaxial bounding the hand would be deviated medially, like the foot, to brace the top of the support, or that it would be placed with the heel at the centerline and the fingers clasping the branch laterally. However, the inked traces and videos uniformly show that hand contacts occur with the heel placed lateral to the centerline of the support, without the pollex abducted or spread from the palm. This occurs during both quadrupedal walking and transaxial bounding. Furthermore, the fact that digital inkmarks are scarcely evident suggests that the lateral fingers provide little traction. Most of the body weight borne by the forelimb is evidently transmitted through the heel and proximal half of the palm, without using any of the conventional grips. Similarly, in the hindlimb, as discussed above, the hallux, which assumes an abducted posture during walking, does not engage in grasping during bounding. Thus, unlike *Callimico*, none of the cheiridia employs grasping when progression is rapid.

The oblique gait and foot positions that typify transaxial bounding may serve to enhance stability in the absence of grasping ability, by orienting the flexion-extension axes of the hindlimb joints at an angle to the line of travel. A familiar functional analogy is the sideways stepping of a person descending a steep incline, where the leg is rotated medially so that lateral aspect of the lead foot acts as a friction brake to slow travel, while the thigh muscles control the kinematics of the upper leg to maintain balance. The foot position adopted in this human behavior resembles that of *L. rosalia* during transaxial bounding.

Callimico hands show none of the elongation unique to *Leontopithecus*. As Hershkovitz (1977) pointed out, the hands of *Callimico* are relatively large and broad, and our impression is that the pads are thicker and the claws are more robust than in *Leontopithecus*. Although it cannot yet be determined whether or not the cheiridia of *Callimico* approximate the ancestral callitrichine pattern, the hands are certainly less specialized in shape and proportions than those of *Leontopithecus*. The hallux and lateral digits in *Callimico* are normally spread wide when contacting the substrate and the hallux appears to be effective in grasping during quadrupedalism. Spread positions of the digits are also maintained during rapid locomotion. Indeed, during bounding-leaps, *Callimico* frequently alter foot placement to take advantage of their pedal grasp. With halluces abducted, they place right and left feet close together to grasp the support between them, rather than relying on the grip of each foot separately. A large fraction of the weight is evidently carried across the halluces and the plantar pads. This paired pattern efficiently concentrates the propulsive thrust of the hindlimb, which is exaggerated in bounding.

The gross frequency distributions of locomotor styles among captive *L. rosalia* and *Callimico* generally resemble one another and wild *Saguinus* as well, yet their locomotor patterns—in kinematics, gait, and hand and foot use—are quite different. Both *L. rosalia* and *Callimico* bound a similar percentage of the time (Fig. 2). However, the dynamics of these classes of locomotor behavior are very different between the two species, and may be related to differences in forelimb morphology, which may in turn be related to differential foraging adaptations (Hershkovitz, 1977; Rosenberger, 1992). The impact of these features on the locomotor behavior of *L. rosalia* only highlights the need to consider behavior within its naturalistic context, and suggests that quantitative studies of locomotion, while useful for describing basic patterns of motor activities, may prove inadequate for illuminating the interrelationships between morphology and behavior except at a general level.

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