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Kinematic Analysis of Trunk-to-trunk Leaping in *Callimico goeldii*

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Leaping to and from vertical trunks is a pattern of locomotor behavior that characterizes the positional repertoire of several prosimian and neotropical primate species. We examined the kinematics of leaping in a group of 6 captive Goeldi's monkeys. We introduced a set of 2 wooden, fixed, noncompliant vertical supports in their enclosure and used 2 video cameras set at right angles to document leaping. The supports are 2.5, 6, or 15 cm in diameter and were placed at distances of between 1 and 2 m. We conducted frame-by-frame analyses of 122 leaps. The results indicate that irrespective of distance leaped and the diameter of takeoff and landing substrates, the forelimbs of Callimico contacted the landing platform in advance of the hind limbs. Moreover, even when leaping a horizontal distance of 2 m, Callimico experienced a downward vertical displacement of only 0.17 m. Several features of the shoulder and forelimb of Callimico appear to be associated with enhanced stability at the humeral head and radioulnar joint, and are consistent with the ability to withstand large compressive forces generated when landing on noncompliant substrates. Based on a series of kinematic equations provided by Warren and Crompton (1998a), the mechanical cost of transport in Callimico (5.4 m/s^{-2}) is greater than those of prosimian vertical clingers and leapers. However, compared to other callitrichine primates, Callimico

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goeldii is behaviorally and anatomically specialized for leaping between vertical trunks in the lowest layers of the forest understory.

INTRODUCTION

Vertical clinging and leaping, or leaping to and from vertical substrates, is a pattern of locomotor behavior that characterizes the positional repertoire of several prosimian genera including *Lepilemur* (Warren and Crompton, 1998a, 1998b), *Avahi* (Warren and Crompton, 1998a, 1998b), *Galago* (Charles-Dominique, 1977; Crompton *et al.*, 1993), *Tarsius* (Crompton *et al.*, 1993; Niemitz, 1984; Peters and Preuschoft, 1984), *Hapalemur* (Grassi, 2001), *Propithecus* (Oxnard *et al.*, 1990), and *Indri* (Tattersall, 1982). Prosimian vertical clingers and leapers maintain relatively long, powerful hind limbs and short forelimbs (Anemone, 1993). Long hind limbs are advantageous to leapers because they extend the duration of time over which the body can be accelerated during takeoff and serve to resist the high kinetic forces of impact when landing hind limbs first on a rigid substrate (Crompton *et al.*, 1993; Demes *et al.*, 1995; Peters and Preuschoft, 1984; Preuschoft, 1985; Terranova, 1996) However, prosimians, e.g., *Otolemur* and *Microcebus*, land forelimbs first during leaping onto horizontal supports.

Trunk-to-trunk leaping requires several mechanical adjustments of limbs, tail, and center of gravity during the takeoff, in-air, and landing phases of travel. They include overcoming considerable inertia when leaping from a noncompliant substrate, generating sufficient impulse (force over time) during takeoff to span the horizontal distance required to reach the landing platform, in-air bodily rotation, and in the case of specialist prosimian leapers, a twisting of the body along the longitudinal axis and concurrent movements of the upper body enabling the hind limbs to be brought forward and strike the landing platform well in advance of the forelimbs (Dunbar, 1988). Forces generated during landing and takeoff can be substantial. Field and experimental data indicate that woolly lemurs (*Avahi occidentalis*, body mass, 708 g) and sportive lemurs (*Lepilemur edwardsi*, body mass, 819 g) generate sufficient force during takeoff to travel a horizontal distance of over 4 m without any loss in vertical height (Warren and Crompton, 1998a). In *Avahi* and *Lepilemur*, rigid or larger diameter supports are used more commonly than compliant or smaller diameter supports as landing and takeoff platforms during the longest trunk-to-trunk leaps (Warren and Crompton, 1998b).

Several species of New World monkeys (Table I) also employ trunk-to-trunk leaping: *Pithecia pithecia* (Fleagle and Meldrum, 1988; Walker, 1993),

Table I. Trunk-to-trunk leaping in New World Primates

Species	Body mass	% Leaps[a]	% Trunk-to-trunk leaps[b]	Intermembral index	Landing
Callimico goeldii	500–550	45.2	55.1	69	Forelimb-first
Cebuella pygmaea	110–120	24.4	37.0	82	NR
Callicebus moloch	950–1020	17.7	12.3	79	NR
Pithecia pithecia	1400–1800	39.7	57.0[3]	75	Hind limb-first
Pithecia monachus	2000–2600	28.4	4.7	77	NR[c]
Saguinus fuscicollis weddelli	325–375	38.6	20.0	79	Forelimb-first
Saguinus fuscicollis nigrifrons	350–410	32.5	19.2	79	Forelimb-first
Saguinus geoffroyi	450–525	41.5	3.8	74	Forelimb-first
Saguinus labiatus	450–500	38.0	8.4	ND	Forelimb-first
Saguinus mystax	525–600	30.9	8.8	76	Forelimb-first
Saguinus tripartitus	NR	33.7	17.5	ND	NR

[a]= percent of travel; [b]= percent of all leaping behavior; [c]= Walker (1993) reports that 20.2% of leaps in *P. pithecia* occurred on what she termed the vertical axis of the tree and an additional 36.8% occurred on boles (trunks); NR = not reported, ND = no data.
Behavioral data on *Callimico*, *S. f. weddelli*, and *S. labiatus* are from Garber and Leigh, 2001.
Behavioral data on *Cebuella*, *Callicebus*, *S. tripartitus*, and *Pithecia monachus* are from Youlatos, 1999. Behavioral data for *Pithecia pithecia* are from Walker, 1993. Behavioral data for *S. geoffroyi*, *S. mystax*, and *S.f. nigrifrons* are from Garber, 1991. Data on intermembral index are from Fleagle, 1999 and Davis, 2002.

Saguinus fuscicollis (Garber, 1991; Garber and Leigh, 2001), *Saguinus tripartitus* (Youlatos, 1999), *Cebuella pygmaea* (Kinzey *et al.*, 1975; Youlatos, 1999; but see Soini, 1988), and *Callimico goeldii*, (Garber and Leigh, 2001; Pook and Pook, 1981, 1982; Porter, 2000). Walker (1993:226) reported that leaping accounts for *ca.* 40% of travel in *Pithecia*, and that during both take-off and landing, *Pithecia* prefers to use a single support which tends to be vertical. In *Pithecia*, as in the case of vertical clinging and leaping prosimians, the hind limbs contact the landing platform first (Walker, 1993). Compared to other pithecine genera, *Pithecia* exhibit long hind limbs relative to forelimb length (Fleagle, 1999).

Field observations of tamarins indicate that during trunk-to-trunk leaping the forelimbs contact the landing support in advance of the hind limbs (Garber, 1991; Garber and Leigh, 2001). Saddle-back tamarins (*Saguinus fuscicollis*) leap to and from vertical trunks more frequently than other tamarin species do (Table I). *Saguinus fuscicollis* is characterized by small body mass (300–400 g), elongated forelimbs, and the highest intermembral index of *Saguinus* spp. (Fleagle, 1999; Jungers, 1985). Forelimb elongation in saddleback tamarins may play an important role in absorbing impact and "decelerating the body when landing on a rigid support" (Garber and Leigh, 2001:28).

Considerably less is known concerning patterns of positional behavior in Goeldi's monkey (*Callimico goeldii*.). *Callimico* remains the least studied genus of neotropical primates (Porter, 2000). Difficulties in studying *Callimico* relate to their circumscribed distribution in Amazonia, a tendency to travel near to the ground, low population density, and cryptic nature (Porter, 2000). However, Garber and Leigh (2001) reported in Brazil that trunk-to-trunk leaping accounted for 55.1% of leaping behavior by *Callimico*. The leaps occur in the lowest levels of the forest undercanopy and 13% were ≥2 m. In addition, *Callimico* is morphologically distinct in possessing elongated hind limbs and the lowest intermembral index of any callitrichine (platyrrhine subfamily that includes *Saguinus*, *Leontopithecus*, *Callimico*, *Callithrix*, *Mico*, and *Cebuella*): Fleagle, 1999). Based on qualitative field observations, like *Saguinus, Callimico* appears to contact the landing substrate forelimbs first during trunk-to-trunk leaping despite clear differences in limb proportions.

In order to more fully understand the kinematics of trunk-to-trunk leaping in *Callimico*, we conducted an experimental study of positional behavior in a captive family group.

Our specific goals are to

1. to describe limb placement and tail orientation during the takeoff, in-air, and landing phases of trunk-to-trunk leaping in *Callimico*;

2. to calculate takeoff and landing velocity and cost of transport during leaping; and
3. to identify relationships among leaping behavior, substrate utilization, and anatomy in Goeldi's monkeys.

METHODS

Subjects, Research Facility and Research Design

We collected video data on trunk-to-trunk leaping in a family group of 6 Goeldi's monkeys (4 adult, 1 subadult, and 1 juvenile; mean adult body mass 468.7 g ± 48.9 g) at the Primate Facility of the Anthropological Institute, University of Zürich, Switzerland. The *Callimico* live in a 60.3-m^3 (6.5 × 3.5 × 2.65 m) outdoor facility that contained natural vegetation and dead tree branches that served as locomotor pathways.

We placed a set of 2 wooden fixed, non-compliant vertical supports in the *Callimico* enclosure. The diameters are 2.5, 6, or 15 cm, i.e., small, medium, and large respectively. We selected them because they are similar to support class sizes used by wild *Callimico* during trunk-to-trunk leaping (Garber and Leigh, 2001; Porter, 2000). Centimeter grids attached to each pole enabled us to record accurately takeoff and landing heights, changes in the relative position of bodily segments—hands, head, feet—and to calculate changes in height-gain or height-loss during each leap. We varied landing and takeoff support diameters and the horizontal distance between vertical poles systematically. The minimum distance between poles was 1 m and the maximum distance was 2 m. Even the smallest poles flexed minimally during landing and takeoff.

We positioned 2 digital 8 video cameras (a SONY DCR – THV 900E PAL, 3CCD Progressive Scan, 48× digital Zoom and a SONY DCR-TRV320-, NTSC, 450× digital zoom) inside the enclosure to document leaping by *Callimico*. Camera 1 was at a fixed distance of 3 m and positioned perpendicular to the direction of the leap. It captured both takeoff and landing phases of each locomotor sequence. The second camera was also perpendicular to the direction of the leap, but 1.3 m from one of the poles. This was done in order to obtain larger close-up images of landings and takeoffs. We used standard NTSC film speed (30 frames per sec). Fields were not separated. Higher film speeds are preferable because they provide greater resolution of all phases of the leap; however, we only included sequences in which full hind limb extension and body angle at takeoff were clearly visible. We collected data over a 2-day span. We used mealworms and raisins to encourage the monkeys to jump between poles. During all

experiments, Anzenberger provided the monkeys with the rewards in order to standardize the height of the food reward and the height at which the subjects contacted the landing platform.

Kinematic Analysis

We measured 7 points and one angle directly from video sequences via NIH Quickimage for Macintosh. The points are: head takeoff and landing height, hand takeoff and landing height, right foot takeoff height, left foot takeoff height, and bipedal landing height. We measured the angle of body takeoff on the frame closest in time to full extension of the hind limbs by following an imaginary line running from the head down the body midline to a vertex at the feet and up the vertical support. We used the complement of the angle in our calculations. We calculated the height gained or lost in flight from the difference of head landing and takeoff vertical positions. We included a minor correction factor to account for slight angling of the recorded video. Additionally, we counted frames from takeoff to landing to estimate horizontal velocity.

We used vertical height change of the head, h; takeoff angle from horizontal, α (alpha); horizontal leaping distance, s; and body mass, M_b; to calculate kinetic energy, E_{KE}; potential energy, E_{PE}; mechanical cost of transport, C; and takeoff (v_o) and landing velocity (v_f) for each leap via kinematics equations similar to those of Warren and Crompton (1998a). Additional variables are: t, calculated flight duration; β (beta), landing angle, v_x, horizontal velocity remaining constant throughout the leap; and v_y, the vertical velocity calculated separately at takeoff and landing.

Initial conditions of the leap are expressed in terms of v_o.

$$v_x = v_o \cos \alpha$$

$$v_y = v_o \sin \alpha - gt$$

with $t = 0$ at takeoff, and $g = 9.80665$ m/s^2 in all calculations.

$$t = \frac{s}{v_x} = \frac{s}{v_o \cos \alpha}$$

$$h = v_y t - \frac{1}{2}gt^2 = v_o \sin \alpha \left(\frac{s}{v_o \cos \alpha}\right) - \frac{1}{2}g \left(\frac{s}{v_o \cos \alpha}\right)^2$$

v_o is then solved for by substitution and simplification.

$$h = s \left(\frac{\sin \alpha}{\cos \alpha}\right) - \frac{gs^2}{2v_o^2 \cos^2 \alpha}$$

$$h = s \tan \alpha - \frac{gs^2}{2v_o^2}(1 + \tan^2 \alpha)$$

$$(s \tan \alpha) - h = \frac{gs^2}{2v_o^2}(1 + \tan^2 \alpha)$$

$$v_o^2[(s \tan \alpha) - h] = \frac{gs^2}{2}(1 + \tan^2 \alpha)$$

$$v_o^2 = \frac{gs^2(1 + \tan^2 \alpha)}{2(s \tan \alpha - h)}$$

$$vo = \sqrt{\frac{gs^2(1 + \tan^2 \alpha)}{2(s \tan \alpha - h)}}$$

Calculations for β (beta) and v_f are as follows.

$$v_x = v_o \cos \alpha$$

$$v_y = v_o \sin \alpha - gt = v_o \sin \alpha - \frac{gs}{v_o \cos \alpha}$$

$$v_f = \sqrt{v_x^2 + v_y^2}$$

$$\beta = \cos^{-1} \frac{v_x}{v_y}$$

We calculated the kinetic energy required for each jump via the following equation and substitution. Body mass is assumed to be 469 g (range 430–540 g) in all cases; it is the mean of the 4 adult *Callimico* subjects.

$$E_{KE} = \frac{M_b}{2} v_o^2$$

$$E_{KE} = \frac{M_b}{2} \left(\frac{gs^2(1 + \tan^2 \alpha)}{2(s \tan \alpha - h)} \right)$$

This simplifies to

$$E_{KE} = \frac{M_b gs^2(1 + \tan^2 \alpha)}{4(s \tan \alpha - h)}$$

We used vertical height change and body mass to calculate potential energy change of each leap.

$$E_{PE} = M_b gh$$

Total mechanical energy of the leap is the sum of E_{KE} and loss in E_{PE}.

We also calculated the cost of transport, a mass and distance standardized measure of mechanical energy:

$$C = \frac{E_{KE} - E_{PE}}{M_b s}$$

Videos from each camera are cross-referenced visually and by time code. We created split screen videos showing footage from each camera simultaneously in Adobe Premiere to better determine and to describe bodily and limb positioning and movements of the tail during flight.

We conducted statistical analyses via Statistica 5.5 (Statsoft Inc., 2000). Due to small sample sizes for particular leaps, nonnormality and heteroscedasticity, we ran nonparametric tests (Mann-Whitney U-test, Kruskal-Wallis test, and Spearman rank correlation) to compare sample distributions. In all analyses statistical significance is $p < .05$.

RESULTS

Trunk-to-Trunk Leaping in *Callimico*

Frame-by-frame analyses of video sequences of trunk-to-trunk leaping in *Callimico* indicate that irrespective of distance leaped and the diameter of takeoff and landing substrates, the forelimbs always contacted the landing substrate in advance of the hind limbs. The takeoff, in-air, and landing phases of leaping in *Callimico* are as follows (Fig. 1A–H). The first forelimb to lose contact with the takeoff substrate is the leading limb and the ipsilateral side of the body is the leading side. For example in Fig. 1A–H: sequence the left forelimb is the leading limb).

Takeoff (Fig. 1A–1C): Leaps began with the monkey adopting a clinging posture on the pole. Its forelimbs are abducted and positioned at or near head height. In preparation for the leap, the spine is flexed, the ventral surface of the body loses contact with the support, the forelimbs are repositioned lower on the support, the leading forelimb (left) loses contact with the support, and the body and head are rotated to sight the landing substrate. As the hind limbs extend, the trailing forelimb loses contact with the support. Given the angle of body rotation at takeoff, the leading hind limb (left) is fully extended while the trailing hind limb (right) provides the final propulsive thrust. The tail is extended horizontally, maintains limited contact with the support, and is positioned on the same side of the body as the leading hind limb.

In-Air (Fig. 1D–1G): Early in the in-air phase of the leap, the hind limbs are fully extended, as is the trailing forelimb. The leading forelimb is pressed against the body, and the tail is positioned on the leading side,
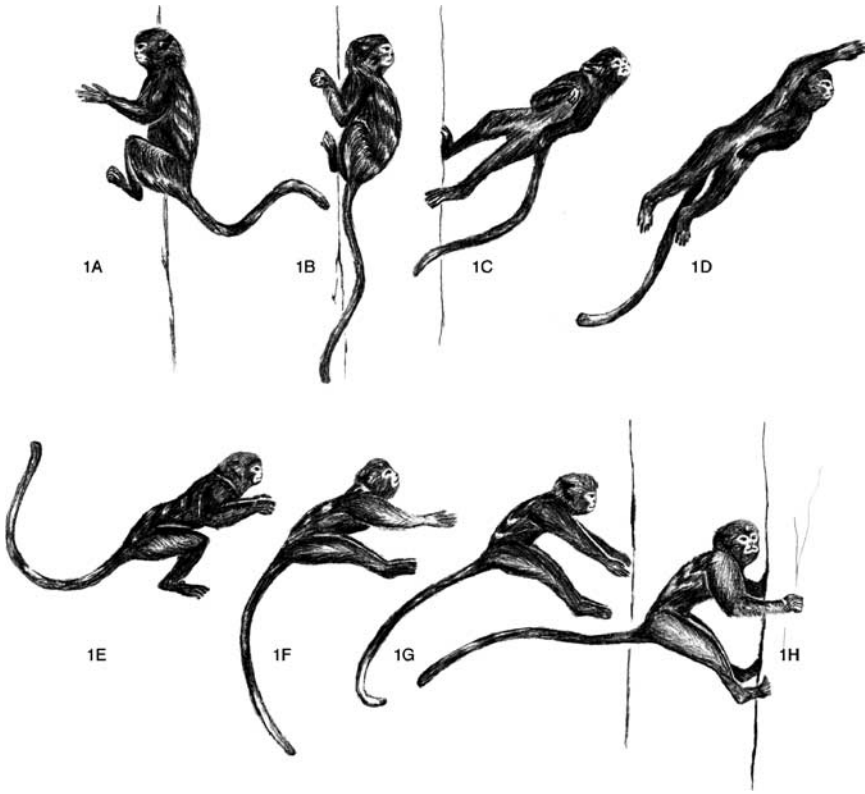
Fig. 1. Trunk-to-trunk leaping in *Callimico goeldii*. Figures are drawn from videotaped locomotor sequences.

hanging well below the level of the body. As the body rotates slightly forward, the tail swings upward and towards the midline of the body. The forelimbs are flexed and abducted, and the hind limbs are flexed and tucked under the body. As the monkey begins to approach the landing substrate the tail adopts a nearly vertical downward orientation, and the forelimbs and hind limbs are fully extended. The dorsal 10–20% of the tail bends forming an almost right angle with the body (pointing to the trailing side). As the forelimbs are positioned far forward of the head, the hind limbs are extended at the hip and the lower limb is slightly flexed. The tail adopts a more horizontal orientation with the distal segment remaining perpendicular (curled and pointing to the trailing side) to the body.

Landing (Fig. 1G–1H): In preparation for landing the forelimbs are fully extended and positioned well in advance of the head. The spine is

flexed, and the hind limbs are extended. The tail is extended horizontally and positioned in the midline of the body. The forelimbs strike the landing substrate in advance of the hind limbs. The partially pronated forelimbs are positioned on either side of the landing support, and are flexed at the elbow. The hind limbs contact the support immediately thereafter. They flex upon impact and the tail is extended and elevated to approximately head height (not shown). Although there was some variation in the position of the tail and limbs during trunk-to-trunk leaping, in all cases the forelimbs contacted the landing substrate before the hind limbs.

Quantitative Analysis of Trunk-to-Trunk Leaping in *Callimico*

We analyzed the kinematics of 122 trunk-to-trunk leaps by *Callimico* over 1–2 m. (Table II). Takeoff velocity and landing velocity are strongly influenced by distance leaped ($p < .0001$). For example, median takeoff velocity of 1-m leaps is 3.3 m/s, whereas median takeoff velocity for 2-m leaps is 4.5 m/s. There is a similar relationship between distance leaped and landing velocity (Table II). When jumping 2 m, median landing velocity is 4.79 m/s, which is 1.4 times the landing velocity of 1-m leaps (3.38 m/s). In leaps of 1 m, 1.6 m, and 1.7 m, takeoff velocity and landing velocity are similar (nonparametric comparison via Wilcoxon matched pairs test). However, in 1.25-m leaps, takeoff velocity significantly exceeded landing velocity ($z = 2.8$, $p = .004$), and in 2-m leaps, landing velocity significantly exceeded takeoff velocity ($z = 2.43$, $p = .014$). The velocities are influenced by several factors including angle of takeoff, height gain/loss during the leap, acceleration due to gravity, the force generated at takeoff, and substrate size. They are not solely a function of distance traveled.

When leaping to and from poles 1.0–1.7 m apart, *Callimico* did not experience a consistent loss in travel height. In fact, during 1.25-m leaps, on average, they gained 0.11 m of vertical height. This was not the case in the longest leaps. When *Callimico* leaped 2 m, they lost 0.17 m in vertical height (Table II). The data highlight the relationship between takeoff and landing velocities and height gain and loss during leaping. For example, takeoff velocity is higher than landing velocity for 1.25-m leaps because it entails substantial gain in height. In contrast, takeoff and landing velocities were similar in leaps of intermediate distance where height gain or height loss was negligible. Finally, in the longest leaps, *Callimico* lost vertical height, and landing velocities significantly exceeded takeoff velocities (Table II).

Takeoff angles reflect the orientation of the body's midline relative to the horizontal in the plane of the leap. They are low when the body is

Table II. Analyses of kinematic data calculated during Trunk-to-trunk leaping in *Callimico* (distances leaped are 1–2 m)

	Overall Median	1 m Median	1.25 m Median	1.6 m Median	1.7 m Median	2 m Median	Kruskal-Wallis Chi-Square	p
n	122	26	38	12	29	17		
alpha (deg.)	35.4	34.6	35.9	36.7	35.6	32.3	8.69	0.0693
beta (deg.)	33.7	32.4	28.1	34.3	35.0	36.8	10.07	0.0392
v_o (m/s)	4.06	3.30	3.87	4.16	4.25	4.49	68.81	<.0001
v_f (m/s)	3.91	3.38	3.62	4.03	4.20	4.79	99.03	<.0001
h (m)	0.041	−0.007	0.112	0.049	0.027	−0.175	17.44	0.0016
E_{KE} (J)	3.86	2.55	3.51	4.06	4.23	4.72	68.81	<.0001
E_{PE} (J)	0.186	−0.034	0.515	0.225	0.125	−0.804	17.44	0.0016
total E (J)	3.58	2.67	3.07	3.81	4.14	5.37	99.03	<.0001
C (m/s^2)	5.33	5.70	5.24	5.08	5.19	5.73	13.93	0.0075

v_o (m/s) = takeoff velocity; alpha (deg) = takeoff angle; v_f (m/s) = landing velocity; beta (deg.) = landing angle; h (m) = the loss or gain in height during the leap; E_{KE} (J) = the kinetic energy of leaping; E_{PE} = the potential energy change of leap; total E = total mechanical energy of leap; C (m/s^2) = the mechanical cost of transport.

nearly horizontal. They are high when the body's midline is close to the vertical takeoff support. Overall, *Callimico* adopted a median takeoff angle of 32–36° and a landing angle of 28–37°. The lowest takeoff angles and highest landing angles are associated with the longest leaps (Table II). However, there is no consistent pattern in bodily orientation and leaping distance because of the influence of vertical height gain and vertical height loss. Our results indicate that takeoff angles were lowest (median = 32.3°) during leaps in which *Callimico* experienced a net loss in vertical height and highest (median = 36.7°) when it resulted in a net gain in vertical height (Spearman $R = .621$ $p < .0001$). Similarly, landing angles were highest (median = 36.8°) when *Callimico* experienced a net loss in height and lowest (median = 28.1°) when leaping resulted in a net increase in height (Spearman $R = -.783$ $p < .0001$).

The unstandardized mechanical energy of leaping increased significantly with distance leaped (Spearman $R = 0.894$, $p < .0001$). The increase in mechanical energy with leaping distance is not linear such that when standardized as the mechanical cost of transport (C), or "the energy required to move the unit mass of an animal one unit distance" (Warren and Crompton, 1998a:87), median energy expenditure was smallest for leaps of intermediate distance and highest for the shortest and longest leaps (Table II, Fig. 2). The cost of transport for 1-m leaps was more variable than the cost of transport for longer distances. *Callimico* leaping 2 m often adopted low takeoff angles, thereby losing more vertical height and potential energy ($p = .0016$).
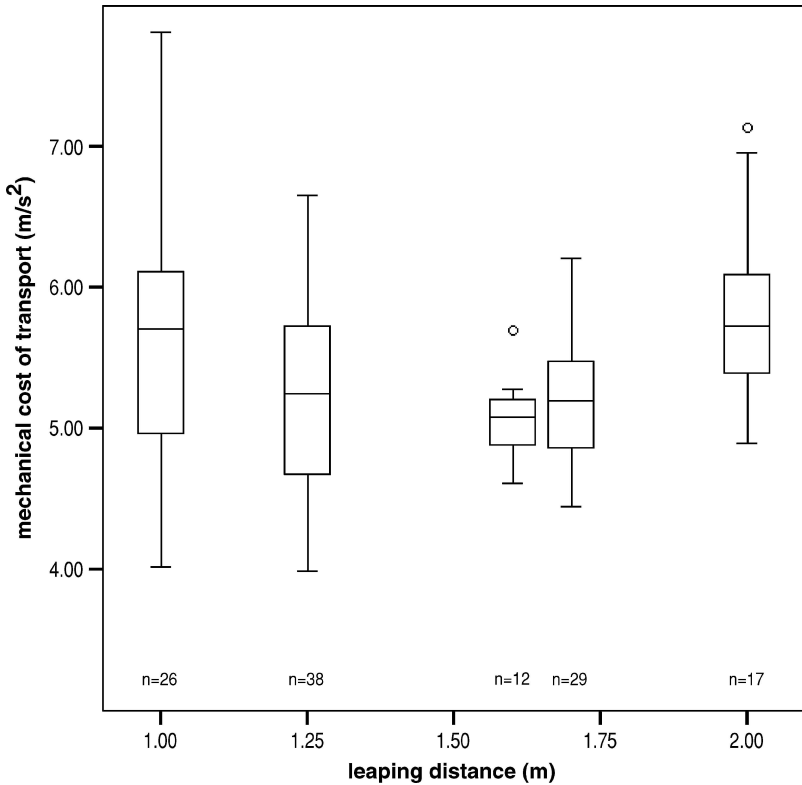
Fig. 2. Mechanical cost of transport (C) and leaping distance in *Callimico*.

The analyses of distance effects without regard to takeoff and landing substrate diameter (Table II) are generally corroborated by focused analyses controlling for substrate size (Table III). We compared kinematics of *Callimico* traveling distances of 1.25 and 1.7 m when leaping to and from medium-sized (6-cm diameter) vertical poles. The results (Table III) indicate significant increases in takeoff and landing velocities and total mechanical energy of leaps at increased distances; however, the mechanical cost of transport is not significantly different. We also examined evidence for differences in the cost of locomotion when leaping between large (15-cm in diameter) and small (2.5-cm diameter) poles 1 m and 1.25 m apart. Holding support size constant during the shorter leaps also produced no significant difference in the mechanical cost of locomotion (Mann-Whitney U; large to small support: 1 m v. 1.25 m, $p = .445$; Small to Large Support 1 m v. 1.25 m, $p = .475$).

Table III. Comparison of Trunk-to-trunk leaping between medium-
Sized vertical substrates located 1.25 and 1.7 m Apart

	1.25 m Median	1.7 m Median	Mann-Whitney U	Mann-Whitney p
n	21	25		
alpha (deg.)	36.0	35.2	245	0.6996
beta (deg.)	31.2	35.1	188	0.1004
v_o (m/s)	3.83	4.25	16	<.0001
v_f (m/s)	3.60	4.23	2	<.0001
h (m)	0.092	0.027	198	0.1548
E_{KE} (J)	3.44	4.23	16	<.0001
E_{PE} (J)	0.423	0.125	198	0.1548
total E (J)	3.03	4.19	2	<.0001
C (m/s^2)	5.17	5.26	235	0.5442

v_o (m/s) = takeoff velocity; alpha (deg) = takeoff angle; v_f (m/s) =
landing velocity; beta (deg.) = landing angle; h (m) = the loss or gain in
height during the leap; E_{KE} (J) = the kinetic energy of leaping; E_{PE} =
the potential energy change of leap; total E = total mechanical energy
of leap; C (m/s^2) = the mechanical cost of transport.

DISCUSSION

New World monkeys exhibit a diverse array of positional adaptations
associated with exploiting resources in arboreal habitals. They include the
parallel evolution of prehensile tails in *Cebus* and the Atelinae, loss of or
reduction of the pollex in *Ateles*, independent movement of the manual
digits in *Cebus*, hind limb elongation and vertical clinging and leaping in
Pithecia, forelimb elongation and tail-forelimb assisted suspensory locomo-
tion in *Ateles*, *Brachyteles*, and *Lagothrix*, and the evolution of elongated
and laterally compressed claw-like nails (tegulae) in tamarins, marmosets
and Goeldi's monkey. In the case of callitrichines, claw-like nails enable
them to cling to and travel on vertical and sharply inclined supports that are
too large to be spanned by their diminutive hands and feet (Garber, 1992).
The use of trunks in callitrichines is best understood as part of a foraging
adaptation associated with the exploitation of resources such as "plant
gums, bark refuging insects, small vertebrates concealed in knotholes, prey
hidden in bromeliads that grow along the main axis of the tree, as well as the
use of vertical trunks to scan for insects and small vertebrates located on the
ground" (Garber *et al.*, 1996:92). More recently, Porter (2000, 2001) found
that fungus is an important food resource consumed by Goeldi's monkey,
particularly during the dry season. *Callimico* exploited fungus in several mi-
crohabitats throughout the forest including the ground, fallen tree branches,
and on bamboo stalks and other vertical trunks (Porter and Garber, 2004).

Field data indicate that leaping accounts for approximately 50% of *Callimico* travel sequences (Garber and Leigh, 2001; Porter, 2000). Although *Callimico* is characterized by several forms of leaping—acrobatic, bounding, and trunk-to-trunk (Garber and Leigh, 2001)—trunk-to-trunk leaping is the predominant form of positional behavior (Buchanan-Smith, 1991; Garber and Leigh, 2001; Pook and Pook, 1981; Porter, 2000). They occur principally 1–3 m above ground in the undercanopy and are initiated from a stationary vertical clinging posture, rather than as part of a rapid sequence of ricochetal movements from trunk to trunk to trunk. Davis (1996:149) described several derived features of the *Callimico* foot (shared with *Pithecia pithecia*, but not with other callitrichines) that "enhance ankle stability during full dorsiflexion and [are] consistent with. . . . vertical clinging and leaping from a vertical platform." Before takeoff (Fig. 1B) *Callimico* crouch. As in *Galago senegalensis* (Aerts, 1998:1619), power is amplified during the takeoff phase of the leap by storing energy via "prestretching [and elastic recoil of particular muscle and tendon groups] during crouching and initial hip extension," which is a countermovement action generating greater force at toe-off (Alexander, 1995). In addition, *Callimico* has relatively long hind limbs and the lowest intermembral index among callitrichine species (Davis, 2002).

It is generally assumed that leaping represents an expensive form of travel (Crompton *et al.*, 1993; Demes *et al.*, 1995), though the costs have not been directly compared with the costs of alternative forms of gap-crossing behaviors. Nevertheless, in some prosimian vertical clingers and leapers, i.e., *Lepilemur edwardsi*, *Avahi occidentalis*, *Tarsius bancanus*, and *Galago moholi*, leaping is estimated to account for 54–87% of total energy costs associated with locomotion (Warren and Crompton, 1998a). Leaping to and from vertical trunks also requires the ability to generate substantial propulsive forces during takeoff and the ability to withstand substantial compressive forces on impact (Peters and Preuschoft, 1984). Given the energetic and biomechanical costs associated with leaping, saltatory species are likely to evolve functional modifications of their musculoskeletal systems in order to increase locomotor efficiency (Crompton *et al.*, 1993; Fleagle and Meldrum, 1988).

We presented captive *Callimico* with opportunities to leap between small, medium and large noncompliant vertical poles 1–2 m apart. Based on an analysis of 122 video sequences, *Callimico* is best regarded as a somewhat less efficient trunk-to-trunk leaper than certain prosimians are. For example, in specialized prosimian vertical clingers and leapers like *Lepilemur edwardsi* and *Avahi occidentalis*, the mechanical cost of transport (C) calculated from kinetic energy is 5.1 m/s^2 and 4.6 m/s^2, respectively (Warren and Crompton, 1998a). Elongated hind limbs in *Lepilemur* and *Avahi* help

to increase the distance/time over which the propulsive forces, required to accelerate the body, are applied to the takeoff platform (Demes and Gunther, 1989; Emerson, 1985), and "provide a long braking distance as a protection against injury in landing" (Peters and Preuschoft, 1984:234). In the case of *Callimico*, the mechanical cost of transport (when calculated from values of kinetic energy) is 5.4 m/s^2, which is greater than that in the prosimians. When leaping a horizontal distance of 1–1.7 m, *Callimico* rarely experienced a reduction in travel height (Table II). However, when leaping 2 m, *Callimico* experienced a downward vertical displacement of 0.175 m. In comparison, Warren and Crompton (1998b) reported that, on average, when leaping a distance of 1.2–1.3 m, *Lepilemur* lost 0.62 m in vertical height and *Avahi* lost 0.88 m in vertical height. When leaping greater horizontal distances (e.g., ≥4 meters), *Lepilemur* and *Avahi* tended to gain height. Warren and Crompton (1998b) argued that it is the energetic cost of leaping longer distances rather than the biomechanical ability to leap longer distances that constrain locomotor behavior in vertical clinging and leaping prosimians. In contrast, it appears that *Callimico* are more biomechanically limited in leaping ability. When leaping 2 m from large noncompliant to noncompliant support, *Callimico* exhibited a marked increase in the cost of transport (Fig. 2). Garber and Leigh (2001) reported that 87% of trunk-to-trunk leaps in wild *Callimico* spanned a horizontal distance of <2 m.

Unlike specialized prosimian vertical clingers and leapers (Terranova, 1996), in *Callimico* the forelimbs contact the landing platform in advance of the hind limbs and absorb the initial force of impact. On average, *Callimico* arrives at the landing platform at a speed of 11.8 km/hr when leaping 1 m and 17.2 km/hr when leaping 2 m. Although in 88% of leaping sequences the forelimbs and hind limbs contacted the landing platform either during the same video frame (29%) or hind limbs in the next video frame (59%), compressive forces associated with landing on noncompliant substrates are large, and we expect there to be features of the forelimb and shoulder girdle in *Callimico* that represent mechanical solutions associated with forelimb-first landing during trunk-to-trunk leaping.

Davis (2002:444, 458) identified several specialized trait complexes in the shoulder and forelimb of *Callimico* that promote "humeral abductor and humeral head stabilization during arm elevation" and "enhance radioulnar stability in partial pronation." Compared to tamarins and marmosets, *Callimico* is characterized by a wide distal radial shaft, a wide ulnar midshaft, and an expanded facet on the proximal radioulnar joint. This last trait is unique to *Callimico*. A wide facet on both the ulna and radius offers enhanced stability during partial pronation of the forearms. During the landing phase of trunk-to-trunk leaping, *Callimico* abduct their forelimbs and partially pronate their forearms when they strike the support.

Increased radial and ulnar shaft width may aid in withstanding compressive forces associated with landing on noncompliant substrates (Lanyon and Rubin, 1985).

Little is known concerning specific differences in the geometry, cross-sectional area, and cortical thickness of forelimb bones in callitrichines. Differences in the distribution of bone mass associated with differences in patterns of positional behavior have been documented among closely related species of lemurs: *Eulemur fulvus* and *Lemur catta* (Ward and Sussman, 1979).

Trunk-to-trunk leaping appears to have evolved independently among several New World primate taxa, including *Pithecia pithecia* (Pitheciinae) and some lineages of tamarins and marmosets (Callitrichinae): *Cebuella pygmaea*, *Saguinus fuscicollis*, *Saguinus tripartitus* and *Callimico goeldii* (Table I) [*Saguinus tripartitus* was once classified as a subspecies of *S. fuscicollis*, and therefore, trunk-to-trunk leaping in these two closely related tamarin species is likely to have a common origin].

Although no quantitative datum is available, marmosets of the genera *Callithrix* and *Mico* (Rylands *et al.*, 2000) appear not to be frequent trunk-to-trunk leapers. Callitrichine trunk-to-trunk leapers differ considerably in body mass, trunk, limb, and hand proportions, and feeding ecology (Bicca-Marques, 1999; Davis, 2002; Garber, 1992; Porter, 2001), and appear to have solved the biomechanical problems associated with this form of transport in different ways. For example, when corrected for body mass, *Callimico* has elongate hind limbs, *Cebuella* has short hind limbs, and *Saguinus fuscicollis* has elongate forelimbs (Garber, 1991; Garber and Leigh, 2001; Jungers, 1985). In addition, given that many trunk-to-trunk leaping callitrichines have close relatives that only occasionally leap from trunk-to-trunk (Table I), and that the most frequent trunk-to-trunk leapers represent highly derived taxa, i.e. *Cebuella* and *Callimico*, it is unlikely that trunk-to-trunk leaping was a dominant form of travel in ancestral Callitrichinae. Moreover, there appears to be no simple relationship between leaping behavior and positional anatomy in callitrichines. We concur with Preuschoft *et al.* (1996:109) that "classic locomotor categories do not describe sufficiently the diverging mechanical demands of locomotion on body shape."

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