

TRUNK-TO-TRUNK LEAPING IN WILD *CALLIMICO GOELDII* IN NORTHERN BOLIVIAPaul A. Garber¹ and Leila M. Porter²¹Department of Anthropology, 109 Davenport Hall, 607 S. Mathews Ave, Urbana, Illinois, 61801, USA p-garber@illinois.edu²Department of Anthropology, Northern Illinois University, Dekalb, Illinois, USA**Abstract**

Compared to other species of tamarins and marmosets, callimicos (*Callimico goeldii*) are characterized by hindlimb and hindfoot elongation, and a pattern of locomotion dominated by leaping to and from vertical supports in the forest understory. We present field data on trunk-to-trunk leaping in a habituated group of callimicos in northern Bolivia. We measured the DBH of the takeoff and landing platform, and the distance traveled during 110 trunk-to-trunk leaps. Our results indicate that mean distance leapt by callimicos was 1.8 m (range 0.2–4.3m). There were no significant differences in the size of takeoff (mean = 10.3 cm) and landing platforms (mean = 9.9 cm). In addition, longer leaps did not occur on larger diameter supports than did shorter leaps. Although tree trunks and saplings were the most commonly used takeoff and landing platforms, 31.8% of the time callimicos jumped to and from bamboo culms. These data highlight the facts that trunk-to-trunk leaping represents a highly specialized pattern of locomotion in callimicos, and that these primates travel through mixed forests that include stands of bamboo and canopy trees. Conservation efforts to sustain viable populations of *Callimico goeldii* must focus on protecting and preserving habitats that contain large tracts of mixed bamboo and secondary forest.

Key Words: callitrichines; locomotion; bamboo; habitat.

Resumen

Comparado con otras especies de tamarinos y monos titís, los callimicos (*Callimico goeldii*) se caracterizan por el alargamiento de sus extremidades posteriores y anteriores, y un patrón de locomoción dominado por los saltos a y desde substratos verticales en el sotobosque. Presentamos datos de campo sobre saltos de tronco a tronco en un grupo habituado de callimicos en el norte de Bolivia. Medimos el DBH de las plataformas de despegue y aterrizaje, y la distancia recorrida durante 110 saltos de tronco a tronco. Nuestros resultados indican que la distancia promedio saltada por los callimicos fue 1.8 m (rango 0.2–4.3m). No hubo diferencias significativas en el tamaño de las plataformas de despegue (promedio = 10.3 cm) y aterrizaje (promedio = 9.9 cm). Adicionalmente, los saltos más largos no ocurrieron en soportes de mayor diámetro que para los saltos más cortos. Aunque los troncos de árboles y arbolitos fueron las plataformas de despegue y aterrizaje más comúnmente utilizadas, el 31.8% del tiempo los callimicos saltaron hacia y desde tallos de bambú. Estos datos resaltan que el saltar de tronco a tronco representa un patrón de locomoción altamente especializado en callimicos, y que estos primates se desplazan a través de bosques heterogéneos que incluyen parches de bambú y árboles de dosel. Esfuerzos de conservación para sostener poblaciones viables de *Callimico goeldii* deben enfocarse en proteger y preservar hábitats que contengan grandes extensiones de bosque de bambú y bosque secundario.

Palabras Clave: callitrichines; locomoción; bambú; hábitat.

Introduction

Tamarins, lion tamarins, marmosets and callimicos represent a highly successful radiation of 7 genera and 42 species of small bodied New World monkeys (Rylands and Mittermeier 2009). These animals exploit a variety of mature, secondary, riparian, successional, highly seasonal, and dry (caatinga, savanna, and cerrado) forest habitats from Panama and across the Amazon basin extending as far south as northern Bolivia and as far east as the Atlantic Coastal forests of Brazil (Hershkovitz, 1977; Rylands, 1996). Despite species specific differences in body mass, hand and limb proportions (Bicca-Marques, 1999; Garber and Leigh, 2001; Davis, 2002), and diet (Digby *et al.*,

2007), field studies indicate that all callitrichine species use their claw-like nails to cling to large vertical and sharply inclined supports in the forest understory (Garber, 1992). These vertical trunks provide a stable foraging platform for the exploitation of resources such as bark refuging insects and small vertebrates, plant exudates, and fungi that grow on bamboo culms (Kinzey *et al.*, 1975; Peres, 1986; Garber, 1992; Youlatos 1999; Porter *et al.*, 2009). Trunks also are used by callitrichines as a perch from which to scan the ground in search of arthropod prey (Garber, 1992).

Although all callitrichines use vertical clinging postures during feeding and foraging, most species do not frequently leap between vertical trunks during travel. For

example, in *Saguinus Geoffroyi*, *Saguinus mystax*, *Saguinus labiatus*, *S. tripartitus*, and *S. fuscicollis* trunk-to-trunk leaping accounts for only 1.5–7.7% of the total positional repertoire during travel (Garber and Leigh, 2001; Garber *et al.*, 2009). In *Cebuella pygmaea*, trunk-to-trunk leaping is more common (12.9% of travel), however, claw climbing, claw clinging, quadrupedal walking/bounding, and leaping on small supports (Youlatos, 1999, 2009) represent its primary modes of travel. In the case of *Callithrix*, detailed quantitative data on positional behavior are lacking, however, travel is generally described as quadrupedal with the majority of leaping restricted to small diameter supports in the tree canopy (Garber *et al.*, 2009).

Callimico goeldii (hereafter referred to as callimicos) is distinct among callitrichines in the degree to which trunk-to-trunk leaping dominates travel. In a field study of positional behavior in callimicos, Garber and Leigh (2001) report that 55.1% of all leaps were between vertical supports in the forest understory. These leaps accounted for 23% of total travel (Garber and Leigh 2001). Similarly, Porter (2004) found that compared to sympatric tamarins, a significantly greater proportion of locomotion in callimicos involved trunk-to-trunk leaping (45% of travel in callimicos vs. 22% for *Saguinus fuscicollis* and 3% for *S. labiatus*). Moreover, relative to other callitrichines, callimicos have elongated hindlimbs that aid in generating large propulsive forces required for leaping from noncompliant supports, and derived features of the ankle that enhance joint stability during takeoff and landing (Garber and Leigh, 2001; Davis, 2002, Garber *et al.*, 2005). Data from a kinematic study of trunk-to-trunk leaping in captive callitrichines indicate that when leaping across a gap of one meter both pygmy marmosets and common marmosets are characterized by a low takeoff velocity and experience significant vertical height loss upon landing (Garber *et al.*, 2009). In contrast, callimicos were found to generate significantly greater velocity at takeoff and to gain or maintain height when leaping these same distances (Garber *et al.*, 2009).

Given that all previous accounts of trunk-to-trunk leaping in wild callimicos are based on visual estimates of the size of takeoff and landing platforms and the distance leaped, we present data using direct measurements of trunk-to-trunk leaping in wild adult callimicos in northern Bolivia. Our goal was to collect detailed observations of leaping in order to better evaluate habitat requirements that are critical for the protection and conservation of this threatened primate in northern Bolivia.

Methods

Study Group and Field Site

During June and July 2005, we collected data on trunk-to-trunk leaping in a habituated group of three callimicos (two adult males and one adult female) inhabiting the forest around Camp Callimico (11°23'S, 69°06'W) in the Department of the Pando, Bolivia (Fig. 1). The forest in

this area is representative of sandy-clay forests of the south and southwestern Amazon Basin (Alverson, 2000), and experiences pronounced dry and rainy seasons (Porter, 2001). Rainfall is approximately 2,000 mm per year (Porter, 2001). Over the course of full day follows, we used a metric tape to systematically measure the diameter at breast height (DBH) of the takeoff and landing platforms used by callimicos, and the distance between them, during 110 trunk-to-trunk leaps. Previous studies at this field site indicate that approximately 80% of all callimico behaviors occur within 5 m of the ground (Porter, 2004), and therefore DBH (taken at a height of 1.5 m) is expected to be a representative measure of the actual size of the support used. Takeoff and landing platforms were scored either as tree trunk or woody bamboo. All three adult group members were fully habituated to the presence of observers and each had been the subject of previous behavioral studies (e.g. Porter *et al.*, 2007). Therefore, we are confident that our presence had a negligible effect on the locomotor behavior or distance leaped by the callimicos. However, given their all black coat color and the lack of individually distinguishable markings or hair patterns, we could not consistently identify individuals. Therefore, data for all three adult individuals were pooled for analyses.

In order to examine the distribution of habitat types within the study group's home range, we divided the forest into habitat categories based on canopy height, visibility criteria, and the dominant plant species present. Using this method, we identified five major habitats: primary forest with open understory, primary forest with dense understory or maturing secondary forest, bamboo forest, secondary forest, and stream edge forest (see Porter *et al.*, 2007). We estimated habitat availability by recording the habitat category present at 100m intervals (102 sample points) along all north-south trails in the group's home range. Comparisons between the size of takeoff and landing platforms were made using a Student's t-Test for paired sample means. Variance in the size of takeoff and landing platforms was compared using an F-Test. Correlations between the size of takeoff platforms, landing platform size, substrate size, and distance leaped were analyzed using regression analyses. In all statistical tests probability was set at <0.05.

Results

We measured 110 leaps in which callimicos traveled between vertical trunks in the forest understory. On average animals were located at 3.0 ± 1.5 m above the ground on the take-off platform. Over 61% of leaps occurred at heights of ≤ 3 m above the ground, and 30% occurred at heights between 3–5 m. The average DBH of trunks used by callimicos as takeoff platforms was 10.3 ± 8.3 cm and the average DBH of landing platforms was 9.9 ± 8.7 cm (Table 1). There were no statistical differences in the diameter ($t = 0.31$, $df = 109$, $p = 0.75$, two-tailed test) or variance in diameter ($F = 0.9$, $df = 109$, $p = 0.29$, one-tailed test) of vertical supports used as takeoff platforms as compared to

supports used as landing platforms. Moreover, DBH of the takeoff platform was not correlated with the DBH of the landing platform ($r=0.04$, $p=0.62$). The culms of woody bamboo (*Guadua weberbaueri*) served as the takeoff substrate in 41.8% of trunk-to-trunk leaps and as the landing substrate in 48.2% of these leaps (Table 1). Overall 40.9% of callimicos' leaps employed tree trunks as both takeoff and landing platforms and 31.8% employed bamboo culms as both takeoff and landing platforms.

Although we did not quantify the relative size distribution of trunks and bamboo culms across the group's 114 ha home range, we did quantify the presence and use of five major habitat types. Our results indicate that despite the

fact that bamboo forest comprised only 5% and secondary forest only 16% of the group's home range, callimicos spent a total of 67% (17% and 50% respectively) of their time in these habitats. In contrast, primary forest accounted for 74% of the callimicos' home range, but was used only 30% of the time. These data highlight that callimicos frequently travel through mixed forests that include stands of bamboo and secondary forest trees, and that large diameter primary forest trees were rarely used as leaping substrates. Less than 3% of takeoff platforms and less than 6% of landing platforms involved vertical trunks with a DBH of greater than 30 cm. Foster and Hubbell (1990) describe trees of greater than 30 cm DBH on Barro Colorado Island, Panama as canopy trees.

Table 1. Trunk-to-trunk leaping in *Callimico goeldii*.

	Leaping Behavior		
	Take Off Platform (DBH in cm)	Landing Platform (DBH in cm)	Distance Leaped (m)
Mean	10.3 ± 8.3	9.9 ± 8.7	1.8 ± 0.8
Range	2.7–71	2.7–71	0.2–4.3
Median	11.0	8.6	1.8
	Substrate Type		
	Sample Size	Sample Size	
Bamboo	46 (41.8%)	53 (48.2%)	
Trunk	64 (58.2%)	57 (51.8%)	

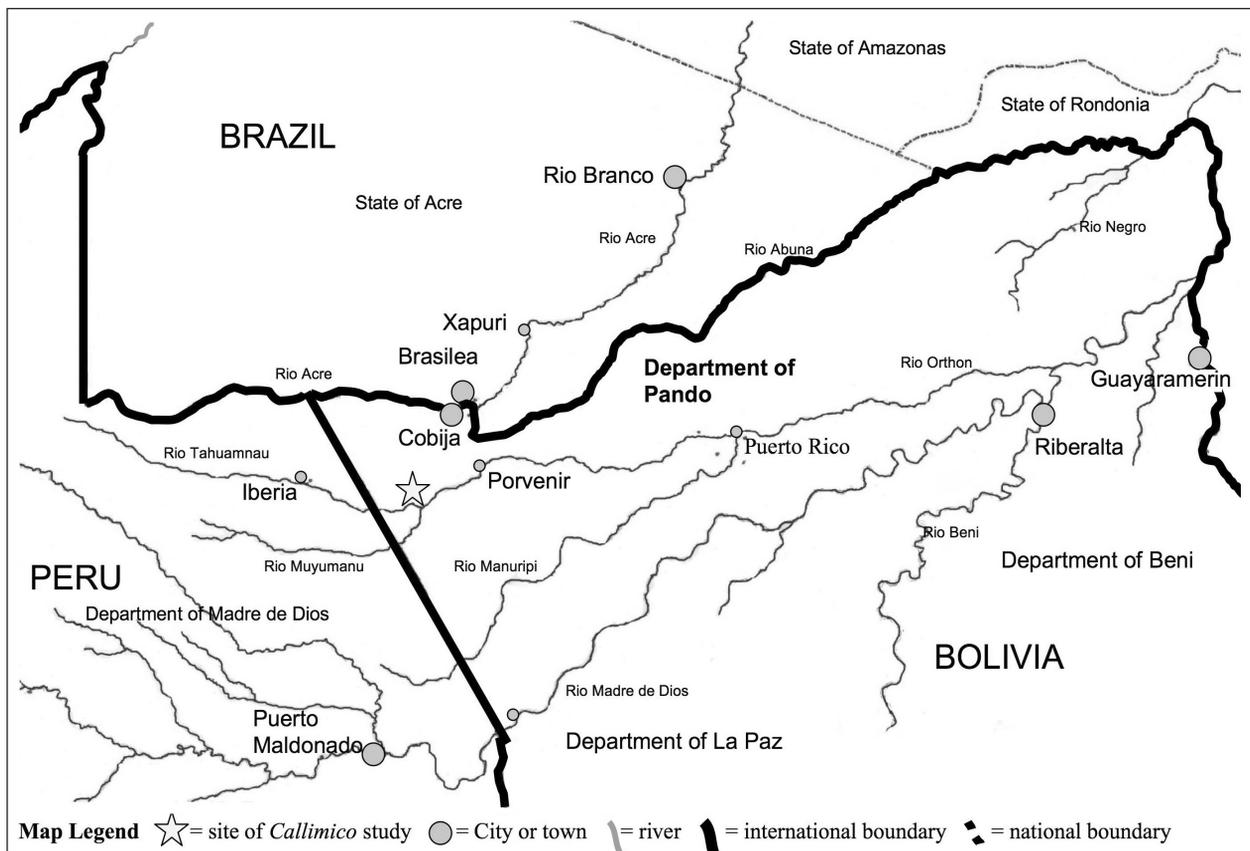


Figure 1. Map of the callimico study site in the Pando region of northern Bolivia.

The mean distance callimicos traveled between vertical trunks was 1.8 ± 0.8 m (Table 1). The shortest leap spanned a distance of 20 cm and the longest leap was 4.3 m. Trunk-to-trunk leaps of 1–2 m (44.5%) and 2–3 m (30.9%) accounted for 75% of all leaps (Figure 2). Less than 1% of leaps were greater than 4 m. During the landing phase of all trunk-to-trunk leaps, callimicos' forelimbs contacted the landing platform in advance of their hindlimbs.

Overall, we found no significant relationship between distance leaped and the size of either the takeoff ($r=0.03$, $p=0.74$) or landing platform ($r=0.001$, $p=0.98$). In addition, the diameter of takeoff and landing platforms used during the shortest leaps (≤ 1 meter) did not differ from those used during the longest leaps (≥ 3 m) (takeoff platform $t=0.25$, $p=0.39$; landing platform $t=-0.02$, $p=0.48$). Table 2 lists the size of takeoff and landing platforms during the shortest and longest leaps. This suggests that given their small body size and elongated hindlimbs, callimicos can generate large propulsive forces pushing off both relatively small (5 cm DBH) and relatively large (71 cm DBH) diameter vertical trunks (Table 1).

We also examined takeoff and landing platform DBH and leaping distance when callimicos traveled on bamboo culms compared to tree trunks (Table 3). As a substrate, bamboo culms were significantly smaller than tree trunks ($t=-9.34$, $p<.0001$). The distance leaped when moving from bamboo culm to bamboo culm (mean of 1.63 m) was marginally shorter than the distance leaped when moving from one tree trunk to another (mean of 2.02 m) ($t=1.95$, $p=0.054$). Moreover, when trunks were used as a takeoff platform (even in cases of trunk to bamboo leaping),

distances leapt were consistently longer than when bamboo culms were used as the takeoff platform ($t=2.47$, $p<0.015$). Although shorter distances leapt when traveling on bamboo may reflect the fact that bamboo culms grow in dense patches, it is also possible that rigid tree trunks provide a more stable takeoff platform during leaping than hollow bamboo culms allowing the animals to leap longer distances.

Discussion

Based on presently available field and captive studies, callimicos appear to be the only callitrichine species characterized by a suite of specialized morphological and behavioral traits associated with trunk-to-trunk leaping (Garber *et al.* 2009). Our results indicate that during trunk-to-trunk leaping callimicos generally leapt distances of 1–3 m (mean = 1.8 m) in the forest understory. These takeoff and landing platforms varied in diameter from approximately 3–71 cm (DBH), however, most leaps occurred on relatively small substrates (mean support diameter = 10 cm) including small trunks, saplings, and bamboo culms. Overall, 59% of all trunk-to-trunk leaps in callimicos involved bamboo culms as either takeoff or landing platforms, and 31.8% of leaps involved bamboo culms as both takeoff and landing platforms. Relative to body mass, callimicos possesses both a highly elongated hindlimb (femur and tibia) and hindfoot (distance from calcaneus to the most distal extent of the metatarsals) compared to other callitrichines (Garber and Leigh, 2001). The callimicos also are characterized by the lowest intermembral index [(ratio of humerus + radius)/(femur + tibia) $\times 100$] of any tamarin or marmoset species (Davis, 2002). Hindlimb elongation has been argued to represent an adaptation for trunk-to-trunk leaping (e.g.

Table 2. DBH of takeoff and landing platforms for the shortest and longest leaps.

	Take Off Platform (DBH in cm)	Landing Platform (DBH in cm)	Distance Leaped (m)
LEAPS ≤ 1 (N = 20)			
Mean	11.6 ± 12.9	10.9 ± 9.3	0.68 ± 0.25
Range	3.5–57.3	2.7–38.8	0.2–1.0
LEAPS $\geq 3M$ (N = 10)			
Mean	10.5 ± 6.0	10.9 ± 8.4	3.42 ± 0.47
Range	4.7–25.1	5.0–33.1	3–4.3

Table 3. Distance leaped to and from different substrates.

	Take Off Platform (DBH in cm)	Landing Platform (DBH in cm)	Distance Leaped (m)
Bamboo to Bamboo (N = 35)	5.13 ± 1.59	5.18 ± 1.76	1.63 ± 0.70
Bamboo to Trunk (N = 11)	4.71 ± 0.98	15.14 ± 7.77	1.52 ± 0.59
Trunk to Bamboo (N = 19)	13.32 ± 6.66	5.07 ± 1.69	1.85 ± 0.70
Trunk to Trunk (N = 45)	14.35 ± 31.36	14.19 ± 34.10	2.02 ± 0.99

“vertical clinging and leaping”) in several species of prosimians (e.g. *Indri*, *Propithecus*, *Avahi*, *Galago*, *Lepilemur*, *Haplemur*, *Tarisus*; Demes *et al.*, 1995; Nekaris and Bearder, 2007) and one other species of New World primate, *Pithecia pithecia* (Walker 1998). Elongated hindlimbs improve leaping abilities as they increase the duration of time over which the body can be accelerated during takeoff (Garber, 2007). In contrast to vertical clinging and leaping prosimians and *Pithecia*, callimicos (and all callitrichines) land forelimbs-first rather than hindlimbs-first (Garber *et al.* 2009). Forelimbs first landings impart high compressive forces on wrist, elbow, and shoulder girdle. How exactly callimicos dissipate these forces remains unclear. However, forelimbs-first landing is common among anthropoids, most of which, are not specialized leapers.

Based on over 1640 hours of observations of our study group from 2002–2006, we estimate that our callimico study group exploited a home range of 114 ha (Porter *et al.*, 2007). Although the home range was composed principally of primary dense understory forest (74%), secondary forest (16%) and bamboo forest (5%), areas of woody bamboo and secondary forest were used by callimicos at significantly greater frequencies than expected based on habitat availability (17% and 50% of observation time respectively) (Porter *et al.*, 2007). Bamboo and secondary forests are characterized by an extremely dense and thorny understory containing considerable numbers of small to medium sized vertical supports. We have previously suggested (Porter and Garber, 2004) that based on their cryptic mode of behavior, black pelage, and virtually exclusive use of the lowest levels of the forest understory, trunk-to-trunk leaping may enable callimicos to reduce predation risk from both aerial and terrestrial predators by concealment and rapid escape. Moreover, bamboo forests provide callimicos with a major component of their diet, *Ascopolyporous*, a fungus that grows exclusively on the culms and branches of woody

bamboo (*Guadua weberbaueri*) (Hanson *et al.* 2006; Porter *et al.*, 2007). Porter and Garber (in prep) report that fungi is consumed by callimicos during both the wet and dry seasons, and accounted for 42% of yearly feeding time. Fifty-eight per cent of the fungi consumed by callimicos in our study group were *Ascopolyporous*.

We conclude that trunk-to-trunk leaping represents a highly specialized pattern of locomotion that distinguishes callimicos from all other callitrichine species. The callimicos’ use of vertical supports in the forest understory appears to be directly tied to its feeding ecology (exploitation of trunks to obtain bamboo fungi and as a foraging platform to locate insect prey), antipredator behavior, and rapid mode of travel. Several species of birds and insects are described as bamboo specialists (Lebbin, 2007) with part or all of their ranges restricted to forests dominated by *Guadua* bamboo. According to Lebbin (2007: 126) Amazonian bamboo habitats are characterized by high primary productivity, and a “combination of rich arthropod resources, a highly distinctive vegetation structure, occurrence across large geographic areas and [exist] in relatively large patches.” Although it remains unclear the degree to which the callimicos’ distribution and feeding ecology are dependent on the presence and availability of bamboo habitats, we suggest that conservation efforts to sustain viable populations of callimicos must focus on protecting and preserving habitats that contain large tracts of mixed bamboo and secondary forest.

Acknowledgments

Funds to conduct this research were provided by the University of Illinois, Urbana, IL, and a National Geographic Research and Exploration Grant, and approved through the UIUC and NIU Institutional Animal Care and Use Committees. The project adhered to the legal requirements for animal research in Bolivia. We thank Edilio Nacimiento Anastacia and Edilio Nacimiento Becerra for assistance in data collection. PAG wishes to thank Chrissie, Sara, and Jenni for their love and support.

References

- Alverson, W., Moskovitz, D., and Shopland, J. editors. 2000. Bolivia: Pando, Rio Tahuamanu. Field Museum, Environmental Conservation, Chicago, IL.
- Bicca-Marques, J. C. 1999. Hand specialization, sympatry, and mixed-species associations in callitrichines. *J. Hum. Evol.* 36: 349–378.
- Davis, L. C. 2002. Functional morphology of the forelimb and long bones in the Callitrichidae (Platyrrhini: Primates). PhD Thesis, Southern Illinois University, Carbondale, Illinois.
- Demes, B., Jungers, W. L., Gross, T. S. and Fleagle, J. G. 1995. Kinetics of leaping primates: influence of substrate orientation and compliance. *Am. J. Phys. Anthropol.* 96: 419–430.

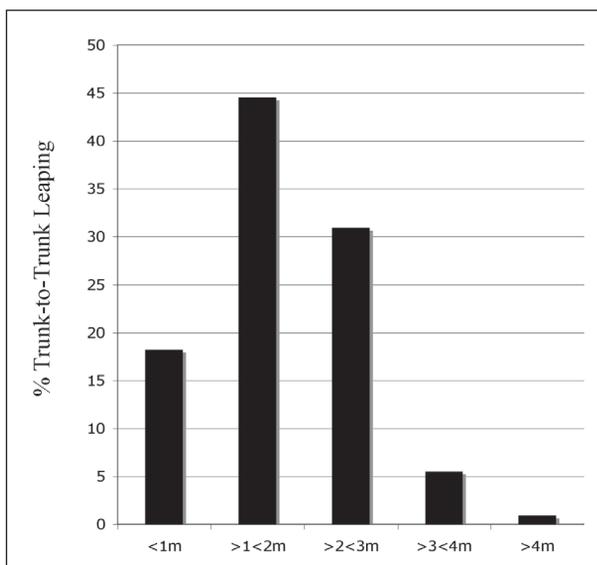


Figure 2. Frequency of trunk-to-trunk leaping in Callimico across different horizontal distances.

- Digby, L. J., Ferrari, S. F., and Saltzman, W. 2007. Callitrichines: the role of competition in cooperatively breeding species. In: *Primates in Perspective*. C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. Bearder, (eds.), pp 85–106. Oxford University Press, Oxford.
- Foster, R. B. and Hubbell, S. P. 1990. The floristic composition of the Barro Colorado Island Forest. In: *Four Neotropical Rainforests*, A. H. Gentry, (ed.). pp 85–98. Yale University Press, New Haven.
- Garber, P. A. 1992. Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *Am. J. Phys. Anthropol.* 88:469–482.
- Garber, P. A. 2007. Primate locomotor behavior and ecology. In: *Primates in Perspective*, C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder (eds). Pp 543–560. Oxford University Press, Oxford, UK.
- Garber, P. A., Leigh, S. R. 2001. Patterns of positional behavior in mixed-species troops of *Callimico goeldii*, *Saguinus labiatus*, and *Saguinus fuscicollis* in northwestern Brazil. *Am. J. Primatol.* 54:17–31.
- Garber, P. A., Blomquist, G., and Anzenberger, G. 2005. Kinematic analysis of trunk-to-trunk leaping in the Goeldi's monkey (*Callimico goeldii*). *Int. J. Primatol.* 26:217–234.
- Garber, P. A., Sallanave, A., Blomquist, G., and Anzenberger, G. 2009. A comparative study of the kinematics of leaping in *Callimico goeldii*, *Callithrix jacchus*, and *Cebuella pygmaea*. In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*. S. Ford, L. Porter, and L. Davis (eds). pp 259–278, Springer Science + Business Media, Inc., New York.
- Hanson, A., Hall, M., Porter, L. and Lintzenich, B. 2006. Composition and nutritional characteristics of fungi consumed by *Callimico goeldii* in Pando, Bolivia. *Int. J. Primatol.* 27:323–346.
- Hershkovitz, P. H. 1977. Living New World Monkeys (Platyrrhini) Vol 1. University of Chicago Press, Chicago, IL.
- Kinzey, W. G., Rosenberger, A. L. and Ramirez, M. 1975. Vertical clinging and leaping in a neotropical primate. *Nature* 255: 327–328.
- Lebbin, D. L. 2007. Habitat Specialization among Amazonian Birds: Why are there so many Guadua Bamboo Specialists. Ph.D. Thesis, Cornell University, Ithaca, NY.
- Nekaris, A. and Bearder, S. K. 2007. The loriform primates of Asia and mainland Africa: diversity shrouded in darkness. In: *Primates in Perspective*. C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder (eds.) pp 24–45. Oxford University Press, Oxford.
- Peres, C. A. 1986. Costs and benefits of territorial defense in golden lion tamarins, *Leontopithecus rosalia*. MA Thesis, University of Florida, Gainesville, Florida.
- Porter, L. M. 2001. *Callimico goeldii* and *Saguinus*: Dietary differences between sympatric callitrichines in northern Bolivia. *Am. J. Phys. Anthropol.* 22:961–992.
- Porter, L. M. and Garber, P. A. 2004. The Goeldi's monkey: a primate paradox? *Evol. Anthropol.* 13:104–115.
- Porter, L. M. and Garber, P. A. in prep. Mycophagy and its influence on habitat use and ranging patterns in *Callimico goeldii*.
- Porter, L. M. 2004. Forest use and activity patterns of *Callimico goeldii* in comparison to two sympatric tamarins, *Saguinus fuscicollis* and *Saguinus labiatus* Am. J. Phys. Anthropol. 124:139–153.
- Porter, L. M., Sterr, S. M. and Garber, P. A. 2007. Habitat use, diet, and ranging patterns of *Callimico goeldii*. *Int. J. Primatol.* 28:1035–1058.
- Porter, L. M., Garber, P. A. and Nascimento, E. 2009. Exudates as a fallback food for *Callimico goeldii*. *Am. J. Primatol.* 71: 120–129.
- Rylands, A. B. 1996. Habitat and evolution of social and reproductive behavior in Callitrichidae. *Am. J. Primatol.* 38: 5–18.
- Rylands, A. B. and Mittermeier, R. A. 2009. The diversity of the New World primates (Platyrrhini): an annotated taxonomy. In: *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation*, P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, and K.B. Strier (eds.), pp. 23–54. Springer Science + Business Media, New York, N.Y.
- Walker, S. E. 1998. Fine-grained differences within positional categories: a case study of *Pithecia* and *Chiropotes*. In: *Primate Locomotion: Recent Advances*, E. Strasser, J. G. Fleagle, A. Rosenberger and H. McHenry (eds.), pp. 31–44. Plenum Press, New York.
- Youlatos, D. 1999. Positional behavior of *Cebuella pygmaea* in Yasuni National Park, Ecuador. *Primates* 40:543–550.
- Youlatos, D. 2009. Locomotion, postures, and habitat use by pygmy marmosets (*Cebuella pygmaea*). In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*. S. Ford, L. Porter, and L. Davis, Springer Science + Business Media, New York.