

## ARTICLES

THE ECOLOGY OF TRUNK-TO-TRUNK LEAPING IN *SAGUINUS FUSCICOLLIS*: IMPLICATIONS FOR UNDERSTANDING LOCOMOTOR DIVERSITY IN CALLITRICHINESP. A. Garber<sup>1,4</sup>, A. C. McKenney<sup>2</sup>, and E. K. Mallott<sup>1</sup><sup>1</sup>Department of Anthropology, University of Illinois, Urbana, Illinois 61801 USA<sup>2</sup>Academic Professional, Department of Anthropology, University of Illinois<sup>3</sup>Editorial Assistant, American Journal of Primatology, Urbana, Illinois 61891<sup>4</sup>Corresponding Author: Paul A. Garber, Department of Anthropology, University of Illinois, Urbana, Illinois 61801, p-garber@illinois.edu, (217) 333-3616 (phone), (217) 244-3490 (FAX)**Abstract**

Several species of callitrichines (tamarins, marmosets, and callimicos) are reported to frequently leap between vertical supports when foraging and traveling in the forest understory. In the present study, we examine trunk-to-trunk leaping in a wild group of four habituated adult saddleback tamarins (*Saguinus fuscicollis weddelli*) in northern Bolivia. From June through July, 2011 we analyzed 200 leaps in which the tamarins moved between vertical supports. On average, takeoff height was 4.1 m ( $\pm 1.3$  m, range 1-7.5 m). During the airborne phase of travel the monkeys lost an average of 0.5 m ( $\pm 0.5$  m) at contact with the landing support, and the mean distance leapt was 1.4 m ( $\pm 0.7$  m). We found no correlation between the diameter at breast height (DBH) of landing and takeoff supports, and either the distance leapt or height gained/lost during leaping. Across callitrichine taxa, it appears that ecological distinctions in diet, patterns of habitat utilization, and predator avoidance strategies have played an important role in understanding the frequency and context of trunk-to-trunk leaping behavior.

**Keywords:** Tamarins, marmosets, positional behavior, vertical clinging and leaping, habitat utilization

**Resumen**

Muchas especies de callitrichinos (tamarinos, titís, y callimicos) se caracterizan por saltar frecuentemente entre substratos verticales durante el forrajeo y los desplazamientos en el sotobosque. En este estudio, examinamos los saltos de tronco a tronco en un grupo habituado de cuatro tamarinos de cabeza amarilla silvestres (*Saguinus fuscicollis weddelli*) en el norte de Bolivia. Durante junio y julio 2011 analizamos 200 saltos de los tamarinos entre substratos verticales. El promedio de la altura de despegue fue 4.1 m ( $\pm 1.3$  m, rango 1-7.5 m). En la fase aérea del salto, los individuos perdieron un promedio 0.5 m ( $\pm 0.5$  m) de altura al llegar al área de aterrizaje y la distancia promedio saltada fue 1.4 m ( $\pm 0.7$  m). No encontramos ninguna correlación entre el diámetro a la altura del pecho (DAP) de los substratos de despegue y aterrizaje, y la distancia saltada o la altura ganada/perdida durante el salto. Las diferencias ecológicas en la dieta, los patrones de uso de hábitat y las estrategias para evitar la depredación, parecen haber jugado un papel importante para entender la frecuencia y el contexto del comportamiento de salto de tronco a tronco en los diferentes taxa de callitrichinos.

**Palabras clave:** Tamarinos, titís, comportamiento postural, salto desde y abrazarse a soportes verticales, utilización del hábitat

**Introduction**

Several species of primates including strepsirrhines, tarsiers, *Pithecia pithecia*, and callitrichines are commonly reported to leap between vertical and/or sharply inclined supports when foraging and traveling in the forest understory (Garber 1991; Demes et al., 1995, 1999; Walker 1998; Youlatos, 1999, 2009; Garber and Leigh, 2001, Crompton et al., 2010). Traditionally, researchers have described this pattern of positional behavior as vertical clinging and

leaping (Napier and Walker, 1967; Kinzey et al., 1975; Gebo, 2011). From a functional perspective, vertical clinging and leaping is composed of two component behaviors: vertical clinging in which an individual adopts a relatively stable upright posture on a trunk or other vertical support, either by grasping the support with their hands and feet or by embedding their claw-like nails into the bark, and leaping between vertical supports which requires powerful and rapid hindlimb extension and propulsion during takeoff, orientation of the body at a subvertical or inclined

angle (45° represents the ballistic optimum, Crompton et al., 2010), and an ability to absorb large compressive forces when landing on a noncompliant substrate (Demes et al., 1995; Garber et al., 2009). Given that clinging to a vertical support and leaping between vertical supports represent two distinct modes of positional behavior, we refer to leaping between vertical supports as trunk-to-trunk leaping.

In this paper we present data on trunk-to-trunk leaping in Weddell's saddleback tamarin, *Saguinus fuscicollis weddelli*, in northwestern Bolivia. Field studies indicate that between 20-89% of leaping in *S. fuscicollis* involves movement to and from vertical supports (Table 1). Saddleback tamarins are the smallest tamarin species, are characterized by forelimb elongation, in particular the distal segments, and possess the highest intermembral index (IMI or the ratio of forelimb length to hindlimb length) among members of the genus *Saguinus* (Falsetti and Cole, 1992; Garber and Leigh, 2001; Davis, 2002). Among callitrichines, trunk-to-trunk leaping is reported to be a major component of the locomotor repertoire in *Callimico goeldii* (callimicos) (Garber and Leigh, 2001; Garber and Porter, 2009), *Cebuella pygmaea*

(pygmy marmosets) (Kinzey et al., 1976; Youlatos (1999, 2009), *S. fuscicollis* (saddleback tamarins) (Garber, 1991; Garber and Leigh, 2001; Nyakatura and Heymann 2010) and *Saguinus tripartitus* (golden-mantled tamarins) (Youlatos, 1999) (Table 1). Given differences among these taxa in body mass (adult female body mass: *C. goeldii* - 468gm, *S. fuscicollis* - 358gm, *C. pygmaea* - 122gm, body mass data for wild *S. tripartitus* are not available; Smith and Jungars (1997), fore- and hindlimb proportions (IMI in *C. goeldii*:70.6, *S. fuscicollis*: 77.1, *C. pygmaea*: 82.3, no data are available for *S. tripartitus*; Davis, 2002), patterns of habitat utilization, and feeding ecology (e.g., bamboo fungi are a dietary staple for *C. goeldii*, trunk exudates are a dietary staple for *C. pygmaea*, and insects, ripe fruits, exudates, and floral nectar are critical components of the diet of *S. fuscicollis* and *S. tripartitus*, reviewed in Digby et al. 2011), we anticipate significant differences in the frequency and context of trunk-to-trunk leaping and the use of trunks as a foraging substrate (Garber et al. 2009).

**Table 1.** Frequency of trunk-to-trunk leaping during travel in callitrichine primates.

Species	Trunk-to trunk leaps (% of locomotor samples)	Trunk-to-trunk leaps (% of all leaps)	Reference
<i>Saguinus fuscicollis nigrifrons</i> <sup>1</sup>	38.4	89.2	Nyakatura and Heymann 2010
<i>Saguinus fuscicollis nigrifrons</i>	24.0	54.5	Norconk 1986
<i>Saguinus fuscicollis nigrifrons</i>	20.8	39.7	Castro 1991
<i>Saguinus fuscicollis nigrifrons</i>	6.1	20.7	Garber 1991
<i>Saguinus fuscicollis weddelli</i>	11.1	67.5	Porter 2004
<i>Saguinus fuscicollis weddelli</i>	6.7	20.0	Garber and Leigh 2001
<i>Saguinus tripartitus</i>	5.8	17.5	Youlatos 1999
<i>Saguinus geoffroyi</i>	1.6	3.8	Garber 1991
<i>Saguinus midas</i>	1.9	7.3	Youlatos unpub. data
<i>Saguinus mystax</i> <sup>2</sup>	8.2	58.9	Nyakatura and Heymann 2010
<i>Saguinus mystax</i>	2.7	8.8	Garber 1991
<i>Saguinus labiatus</i>	2.8	8.4	Garber and Leigh 2001
<i>Saguinus labiatus</i>	2.3	10.9	Porter 2004
<i>Leontopithecus rosalia</i> <sup>3</sup>	2.8	8.9	Stafford et al. 1996
<i>Callimico goeldii</i>	23.1	55.1	Garber and Leigh 2001
<i>Callimico goeldii</i>	47.4	88.6	Porter 2004
<i>Callithrix jacchus</i> <sup>4</sup>	0.6	2.9	Youlatos unpub. data
<i>Cebuella pygmaea</i>	12.9	35.1	Youlatos 1999
<i>Cebuella pygmaea</i>	15.3	36.7	Youlatos 2009

<sup>1</sup>- Data from this study of *S. fuscicollis nigrifrons* were extrapolated based on Table 1 and Figure 1 from Nyakatura and Heymann (2010). These authors do not provide quantitative data on both takeoff and landing platform orientation during leaping but state "almost all leaps were associated with vertical clinging and leaping behavior" (page 246).

<sup>2</sup>- Data from this study of *S. mystax* were extrapolated based on Table 1 and Figure 1 from Nyakatura and Heymann (2010). These authors do not provide quantitative data on both takeoff and landing platform orientation during leaping but state "Leaps occurred mostly on vertical inclines from trunk to trunk (vertical clinging and leaping behavior), but were also observed on other inclines, often connecting terminal branches of different trees. *S. mystax* displayed much less vertical clinging and leaping than *S. fuscicollis*" (page 246).

<sup>3</sup>- Data for wild *Leontopithecus rosalia* were extrapolated from data presented in Figure 4 and Table 5 from Stafford et al. (1996) and include leaps in which trunks were used either as landing or takeoff platforms.

<sup>4</sup>-Data for *Callithrix jacchus* based on preliminary observations of a semi-natural group inhabiting the Botanical Gardens, Rio de Janeiro, Brazil.

## Methods

During June and July, 2011, we collected behavioral and ecological data on a group of four adult saddleback tamarins (*S. fuscicollis weddelli*, three adult males and one adult female) inhabiting a mixture of primary forest, maturing secondary forest, bamboo forest, disturbed secondary forest, and stream edge forest in the Department of the Pando in northern Bolivia (Camp Callimico, 11°23'S, 69°06'W). This area of the Amazon Basin experiences pronounced dry and rainy seasons (with rainfall averaging approximately 2,000 mm per year, Porter, 2001).

On 7 of 22 full-day follows, we opportunistically recorded a total of 200 trunk-to-trunk leaps. Our study group of saddleback tamarins was fully habituated to the presence of observers, and had been the focus of previous studies in 2008 and 2009 (Porter and Garber, 2011). To ensure that our presence had a negligible effect on tamarin locomotor behavior or the distance leapt, we followed the monkeys daily for a period of two weeks prior to collecting data on leaping. For each leap the following information was collected: takeoff and landing height, the horizontal distance leapt, support type, height gained or height lost during travel, and diameter at breast height (DBH) of takeoff and landing supports. All measurements were taken immediately after we observed the tamarin to leap. Takeoff height and landing height were estimated by placing a 1.5 m tape on the substrate for scale. Height gain or height loss during a leap was calculated as takeoff height minus landing height. However to be conservative, in our analyses we consider height gains or height losses of  $\pm 0.25$  m to reflect horizontal travel (no effective change in height). DBH was measured using a metric tape.

Takeoff and landing supports were scored either as tree trunk, liana, or woody bamboo. All vertical supports leapt to and from were considered in our analysis (we did not have a size threshold). The horizontal distance leapt was calculated by measuring the distance between the landing and takeoff supports using a metric tape. Finally, a support was considered compliant if we could detect it to move or be displaced during a tamarin leap. We acknowledge that this is a highly qualitative measure of support compliance. In order to examine whether the distribution of substrate type, DBH, and inter-tree distances within the study group's home range influenced tamarin support preference and leaping behavior, we walked two 100 × 2 meter transects running east-west between marked trails and measured every vertical support with a DBH >2.5 cm and a height of >2.0 m that was present inside the transect (N=406) (West, 2004). At every 20<sup>th</sup> support (N=20 target trees), we marked an area that formed a semicircle with a radius of 3 meters with the target tree at the midline of its base. We then counted the number and measured the DBH of vertical lianas, trunks, and bamboo culms that were located within the 9.42 m<sup>2</sup> area (total area sampled for 20 target trees was 188.4 m<sup>2</sup>). For each vertical support present in

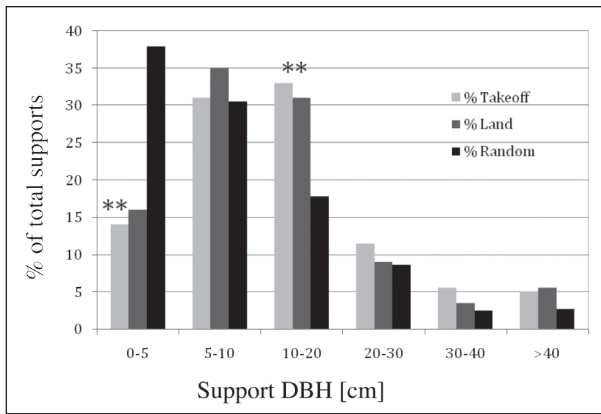
the semicircle (total = 71) we also measured the horizontal distance from the midpoint of the base of the semicircle to each tree (distance between focal tree and sample tree). We selected a radius of 3 meters because approximately 94% of trunk-to-trunk leaps in saddleback tamarins were less than 3 meters in horizontal distance (see Results).

Given that the data were not normally distributed, comparisons between the DBH of takeoff and landing supports were made using the nonparametric Mann-Whitney U-test. Comparisons between the DBH of vertical supports in our sample transects and the DBH of supports used by the tamarins for leaping also were evaluated using a Mann-Whitney U-test. Variance in the size of takeoff and landing supports was compared using an F-Test. The effects of takeoff support DBH, landing support DBH, and the distance leapt on height gained/lost during leaping were analyzed using multiple regression analysis, as were the effects of the takeoff support DBH, landing support DBH, and height lost/gained during leaping on the horizontal distance leapt (SAS v9.3, SAS Institute, 2011). Probability values of  $p \leq .05$  are considered significant.

## Results

### *Support type and support diameter*

Saddleback tamarins commonly foraged and traveled on tree trunks in the forest understory. We did not observe the tamarins to leap between vertical branches in the middle or upper levels of the tree crown. Trunks were used as both takeoff and landing supports in approximately 90% of leaps. Areas of bamboo forest were uncommon in the study group's home range and bamboo culms accounted for less than 0.25% of vertical supports present in our sample transects. We did not observe the tamarins to leap to or from bamboo culms. Lianas accounted for 14% (57/407) of the vertical supports present in our vegetation transects, however, they were used by the tamarins as takeoff supports during only 7.5% of leaps ( $X^2=6.0$ ,  $df=1$ ,  $p<.05$ ) and as landing supports in 10% of leaps ( $X^2=2.2$   $df=1$ ,  $p>.20$ ). We found that in 7 of 15 leaps in which lianas served as takeoff supports, the liana moved or was displaced by the leaping tamarin. In each case the liana had a DBH of  $\leq 5$  cm. In 7 of 20 leaps in which lianas served as a landing support, the liana also was compliant. In each of these cases the liana had a DBH of  $\leq 5$  cm (however, there were two instances in which the tamarins landed on a liana with a DBH  $\leq 5$  cm and the support was judged not to be compliant. Tree trunks were rarely compliant; 1.0% of takeoff and 2.7% of landing supports). Overall, lianas were significantly smaller in diameter than were tree trunks (lianas =  $5.48 \pm 2.8$  cm DBH; range 2.5-16.2 cm vs. tree trunks =  $11.3 \pm 12.6$  cm DBH; range 2.5-103.5 cm; Mann-Whitney U-test,  $Z=5.57$ ,  $p<.0001$ ), and this may have affected the tamarins' use of lianas as leaping supports. As indicated in Fig. 1, tamarins used vertical supports of less than 5 cm DBH as either takeoff ( $X^2=30.0$ ,  $df=1$ ,  $p<.001$ ) or landing supports ( $X^2=25.3$ ,  $df=1$ ,  $p<.001$ ) less frequently than expected based on their



**Figure 1.** Diameter at breast height (DBH) of the pattern of vertical support use by saddleback tamarins compared to the availability of vertical supports in their home range. \*\*:  $p < .001$

availability. In contrast, the monkeys exhibited a preference for leaping to and from supports of between 10-20 cm DBH ( $X^2=26.4$ ,  $df=1$ ,  $p < .001$  for takeoff support;  $X^2=19.9$ ,  $df=1$ ,  $p < .001$  for landing support). Overall, we found no significant difference between the mean DBH of takeoff ( $15.7 \text{ cm} \pm 16.3$ ) and landing supports ( $15.2 \text{ cm} \pm 17.8$ ; Mann-Whitney U-test,  $Z = 1.21$ ,  $p=0.22$ ) selected by the tamarins.

#### Height gained/height lost

During 200 trunk-to-trunk leaps, the height of the tamarins' takeoff support ranged from 7.5m to 1m above the ground. Mean takeoff height was 4.1 m ( $\pm 1.3$  m). During 30% of takeoffs the tamarins were positioned at a height of between 4-5m and during 30% of the landings the tamarins were positioned at a height of between 3-4 m. (Table 2). During their airborne phase of travel, the monkeys experienced a loss in height during 121 leaps (60.5%), retained a relatively horizontal trajectory during 70 leaps (35%), and gained height during only 9 leaps (4.5%). The greatest vertical distance lost during a leap was 2.2 m and the greatest gained was 0.7 m. On average, the saddleback tamarins lost 0.5 m ( $\pm 0.5$  m) in height when leaping between vertical supports. During all trunk-to-trunk leaps, saddleback tamarins landed forelimbs first, a behavioral pattern which is consistent across callitrichines.

#### Distance leapt

The average horizontal distance leapt by the tamarins was 1.4 m ( $\pm 0.7$ ), with the greatest number of leaps spanning a distance of 1-2m (51.5%) (Table 3). In our sample, 9.5% of leaps were  $< 0.5$ m in distance and 2.0% spanned a distance of greater than 3 meters (Table 3). Given that our measure of horizontal distance leapt was identical to the way we measured the spatial distribution of vertical supports in our sample plots, we compared these data sets to determine whether the tamarins selected nearer or further vertical supports for leaping. We found that the horizontal distance leapt by the tamarins between vertical supports differed significantly from the spatial distribution of these supports in our focal transects ( $1.90 \pm 0.84$  m;  $N=71$ ;

**Table 2.** Takeoff and landing height during trunk-to-trunk leaping in *Saguinus fuscicollis weddelli* ( $N=200$  leaps)

Height (meters)	Takeoff Platform (%)	Landing Platform (%)
$< 1$	0.5	0.5
$\geq 1 < 2$	2.5	7.0
$\geq 2 < 3$	13.0	21.5
$\geq 3 < 4$	21.5	30.0
$\geq 4 < 5$	30.5	25.0
$\geq 5 < 6$	21.0	10.5
$\geq 6 < 7$	9.5	5.0
$\geq 7$	1.5	0.5

**Table 3.** Distance leaped and height gain/loss in *Saguinus fuscicollis weddelli* during trunk-to-trunk leaping

Distance leaped (m)	Height change (cm)	Sample size	% Leaps with height loss <sup>1</sup>	% Leaps with height gain <sup>1</sup>
$\leq 1$	$-22 \pm 43$	61	31.1	8.2
$> 1 \leq 2$	$-49 \pm 44$	103	67.0	3.8
$> 2 \leq 3$	$-104 \pm 55$	32	90.6	0.0
$> 3$	$-150 \pm 46$	4	100.0	0.0

1- in our analyses we consider height gains or height losses of  $\pm 0.25$  m to reflect horizontal travel (no effective change in height)

Mann-Whitney U-test,  $Z=4.17$ ,  $p < .0001$ ). These data suggest that given the option of leaping between nearer or more distant vertical supports, especially those separated by a distance of approximately 2 meters, saddleback tamarins preferred to jump to and from nearer supports.

Finally, using multiple regression we examined the effects of support DBH and height gained or lost on distance leapt. The multiple regression analysis for height lost during leaping ( $R^2=0.3802$ ) showed a significant effect with increasing distance ( $t=10.921$ ,  $p < .0001$ ). As indicated in Table 3, in 68.8% (42/61) of leaps of less than 1 meter, the tamarins either maintained (60.6%) or gained (8.2%) height, whereas in 67% of leaps (69/103) between  $1 \geq 2$  meters, 90.6% of leaps (29/32) between  $2 \geq 3$  m, and 100% (4/4) of leaps  $> 3$  meters, the tamarins lost height. In contrast, takeoff support DBH ( $t=0.542$ ,  $p=0.5888$ ) and landing support DBH ( $t=0.959$ ,  $p=0.3387$ ) did not significantly predict height loss/gain during leaping. Saddleback tamarins did not select landing supports of smaller (and potentially more compliant) DBH during longer leaps nor did they select more larger and more stable landing supports with an increase in leaping distance (Mann-Whitney U-test,  $Z = 0.39$ ,  $p=.696$ ; Table 4). Similarly, a multiple regression examining the effects of takeoff support DBH ( $t=1.34$ ,  $p=0.1813$ ) and landing support DBH ( $t=0.68$ ,  $p=0.4961$ ) did not significantly predict distance leapt. Thus, the DBH of takeoff and landing supports did not appear to be a critical factor influencing trunk-to-trunk leaping in saddleback tamarins.

**Table 4.** Support diameter, horizontal distance leapt and height gain/loss during trunk-to-trunk leaping in *Saguinus fuscicollis weddelli*.

Takeoff Platform					
DBH	N	Distance leapt	Range	Height Gain/Loss	Range
≤5 cm	28	1.18±0.71	0.20-2.60	-0.40±0.59	-2.25-0.5
>5≤10	62	1.47±0.74	0.48-3.37	-0.46±0.56	-1.75-0.75
>10≤20	66	1.48±0.61	0.36-3.37	-0.60±0.58	-2.0-0.5
>20≤40	34	1.61±0.81	0.38-3.68	-0.60±0.45	-1.5-0.5
>40≤80	7	0.98±0.40	0.43-1.75	-0.46±0.24	-0.75-0.0
>80	3	0.77±0.26	0.49-1.02	-0.08±0.14	-0.25-0

Landing Platform					
DBH	N	Distance leapt	Range	Height Gain/Loss	Range
≤5 cm	32	1.41±0.72	0.20-2.86	-0.46±0.49	-1.5-0.25
>5≤10	70	1.38±0.77	0.23-3.68	-0.47±0.61	-2.25-0.75
>10≤20	62	1.49±0.66	0.33-3.37	-0.56±0.54	-2.0-0.5
>20≤40	24	1.52±0.69	0.42-2.84	-0.61±0.56	-1.75-0.5
>40≤80	6	1.11±0.39	0.55-1.75	-0.55±0.17	-0.75-(-0.25)
>80	5	1.36±0.54	0.81-1.90	-0.55±0.41	-1.0-(-0.25)

## Discussion

Leaping is a dominant form of travel in all species of tamarins, marmosets, and callimicos, and in general, three types of leaping behavior have been described for these small-bodied primates (Garber, 1991; Youlatos, 1999, 2009; Garber and Leigh, 2001; Nyakatura and Heymann, 2010). These are acrobatic leaps (also called terminal leaps by Youlatos, 2009) which begin and end on thin terminal supports in the periphery of the tree crown and between the crowns of adjacent trees, bounding leaps which are an outgrowth of rapid quadrupedal travel and occur principally on moderate and large diameter horizontal and oblique supports, and trunk-to-trunk leaps which occur on small, moderate, or large sized vertical or sharply inclined supports in the forest understory. However, there exists marked variability among callitrichine species in body mass, limb and body proportions, and the frequency of different forms of positional behavior (Table 1). An understanding of these differences offers critical insight into patterns of habitat utilization, feeding ecology, and locomotor anatomy in this primate radiation.

Among callitrichines, *C. goeldii*, *C. pygmaea*, and *S. fuscicollis* are the most frequent trunk-to-trunk leapers (Table 1). In the case of callimico, the exploitation of resources (fungi) present both in bamboo forest (which is dominated by vertical supports) and on decaying logs and fallen trunks, a behavioral pattern of crypticity and rapid escape, and anatomical adaptations associated with hindlimb elongation and ankle stability during dorsoflexion (Davis, 1996), help to explain the high frequency of long trunk-to-trunk leaps reported in this species (Garber and Porter, 2009; Porter and Garber, 2010). In contrast, the diet of pygmy marmosets is dominated by the consumption of plant exudates

that are found in inundated forests along stream margins and in dense liana forest (Rylands, 1996; Youlatos, 2009). Youlatos (2009) reports that during feeding, 84.2% of locomotor behavior (principally claw climbing) and 85.7% of postural behavior (principally claw clinging) in *Cebuella* involved the exploitation of vertical trunks. In contrast to callimicos, the majority of trunk-to-trunk leaps in wild pygmy marmosets spanned a horizontal distance of less than 0.5 meters, with only 3% greater than 1 m (Youlatos pers. comm, Youlatos, 2009). This may reflect the fact that pygmy marmosets are characterized by extremely short hindlimbs, even when adjusted for body size (Davis, 2002). Moreover given that peak leaping forces scale to body mass<sup>(-1/3)</sup>, and increase with distance leapt, smaller bodied primates are expected to engage in a series of shorter leaps in order to reduce mechanical stresses on their musculoskeletal system (Demes et al., 1999).

In the present study we analyzed 200 trunk-to-trunk leaps in Weddell's saddleback tamarins (*S. fuscicollis weddelli*). Relative to other tamarin species, *S. fuscicollis* (and possibly *S. tripartitus* and *Saguinus nigricollis*; all three of these taxa are members of the *S. nigricollis* group; Mataushek et al., 2011) travel and feed more commonly in the forest understory and use trunks as a perch to scan the ground for insect and small vertebrate prey, and to explore tree holes and bark crevices (Garber, 1992, Porter, 2001). In addition, exudates are reported to account for between 7.6-30.3% of saddleback tamarin feeding time (Table 7.2 in Digby et al., 2011). During exudate feeding, saddleback tamarins commonly cling to vertical trunks in the forest understory (Garber, 1993). We found that saddleback tamarins leapt to and from vertical supports that varied in DBH from 2.8 cm to over 110 cm, with 64% of takeoff supports and 66% of landing supports >5≤20 cm DBH. The majority



of leaps occurred in the under canopy (at a height between 1 and 5m), with 30% spanning a horizontal distance of  $\leq 1$ m, 51.5%  $\geq 1 < 2$ m, and 18%  $\geq 2$  m. As distance leapt increased, the tamarins lost a greater amount of height (Table 3). Few of the takeoff or landing supports used by saddleback tamarins were compliant, and support DBH was not correlated with distance leapt or height gained or lost during leaping. This same pattern has been reported in wild *C. pygmaea* (Youlatos, 2009) and wild *C. goeldii* (Garber and Porter, 2009). Thus, it appears that among both smaller bodied and larger bodied callitrichines support DBH is not a critical factor influencing trunk-to-trunk leaping. This may reflect the mechanical advantage claw-like nails provide in maintaining support on vertical branches that otherwise are too large to be grasped by their relatively small hands and feet (Garber, 1992).

In the present study, wild saddleback tamarins were found to leap relatively longer distances between vertical supports than do wild pygmy marmosets and relatively shorter distances than wild callimicos (Youlatos, 2009, Garber and Porter, 2009). Approximately 18% of the leaps we recorded in wild saddleback tamarins spanned a horizontal distance of  $> 2$  m. However, during these longer leaps tamarins' experienced considerable height loss (average height loss of  $> 1$ m when leaping a horizontal distance of greater than 2m, Table 3, compared to a height loss of 17.5 cm in callimicos leaping a distance of 2m), which is expected to result in an increase in compressive forces acting on their forelimbs during landing. This is supported by the fact that during trunk-to-trunk leaping, height loss in callitrichines is negatively correlated with takeoff velocity and positively correlated with landing velocity (Garber et al., 2009). In this regard, Garber and Leigh (2001:28) have suggested that forelimb elongation in saddleback tamarins (relative to other *Saguinus* species) may function to "increase[ing] the braking distance available for decelerating the body when landing on a rigid support" and more effectively dissipate the high forces generated on impact.

In conclusion, although all species of callitrichines cling to and travel on relatively large vertical supports using their claw-like nails, only a small number of taxa, most notably *C. goeldii*, *S. fuscicollis*, and *C. pygmaea*, are reported to commonly leap between vertical supports in the forest understory. These three species differ markedly in diet, body mass, limb proportions, and the kinematics of leaping. Detailed studies of positional behavior are needed on marmosets of the genera *Mico*, *Callithrix*, and *Callibella*, and in other *Saguinus* species, to better understand the functional and ecological implications of callitrichine postcranial anatomy on vertical clinging, patterns of leaping, and species differences in habitat utilization.

## Acknowledgments

We thank the Ministerio de Medio Ambiente, Colección Boliviana de Fauna, Bolivia for granting us permission to conduct research at the field site. This study complied with the guidelines governing nonhuman primate research at the University of Illinois and the laws of Bolivia. Funds to conduct this research were provided by the Center for Latin American and Caribbean Studies at the University of Illinois. We wish to thank Leila Porter, Edilio Nascimento, and Ruth Cuadiay for assistance in Bolivia in habituating and monitoring the saddleback tamarins. We also thank Dionisios Youlatos for allowing us to cite his unpublished data on positional behavior in *Saguinus midas* and *Callithrix jacchus*, and Michelle Bezanson for providing comments on an earlier draft of this manuscript. Nicoletta Righini translated the abstract into Spanish. Finally, without the love and support of Sara and Jenni none of this would be possible.

## References

- Castro, N.R. 1991. Behavioral ecology of two coexisting tamarin species (*Saguinus fuscicollis nigrifrons* and *Saguinus mystax mystax*, Callitrichidae, Primates) in Amazonian Peru. Doctoral thesis. Washington University, St. Louis, MO.
- Crompton, R.H., Blanchard, M.L., Coward, S., McNeill Alexander, R. and Thorpe, S.K. 2010. Vertical clinging and leaping revisited: Locomotion and habitat use in the Western Tarsier, *Tarsius bancanus* explored via loglinear modeling. *Int. J. Primatol.* 31: 958–979.
- Davis LC. 1996. Functional and phylogenetic implications of ankle morphology in Goeldi's monkey (*Callimico goeldii*). In: *Adaptive Radiations of Neotropical Primates*, M. Norconk, A.L. Rosenberger, and P.A. Garber (eds.), pp. 133–156. Plenum Press, New York.
- Davis, L.C. 2002. Functional morphology of the forelimb and long bones in the Callitrichidae (Platyrrhini, Primates). Doctoral 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: 419–429.
- Demes, B., Fleagle, J.G. and Jungers, W.L. 1999. Takeoff and landing forces of leaping strepsirrhine primates. *J. Hum. Evol.* 37: 279–292.
- Digby, L.J., Ferrari, S.F. and Saltzman, W. 2011: Callitrichines: the role of competition in cooperatively breeding species. In: *Primates in Perspective. 2nd Edition*, C.J. Campbell, A. Fuentes, K.M. MacKinnon, S.K. Bearder and R.M. Stumpf, (eds.), pp. 91–107. Oxford University Press, Oxford, UK.
- Falsetti, A.G. and Cole III, T.M. 1992. Relative growth of postcranial skeleton in callitrichines. *J. Hum. Evol.* 23:79–92.

- Garber, P.A. 1991. A comparative study of positional behavior in three species of tamarin monkeys. *Primates* 32: 219–230.
- 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. 1993. Feeding ecology and behaviour of the genus *Saguinus*. In: *Marmosets and Tamarins: Systematics, Ecology and Behaviour*, A.B. Rylands (ed.), pp. 273–295. Oxford University Press, Oxford, UK.
- Garber, P.A. and Leigh, S.L. 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., 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.M. Ford, L.M. Porter, and L.C. Davis (eds.), pp. 259–278. Springer Press, New York.
- Garber, P.A. and Porter, L.M. 2009. Trunk-to-trunk leaping in wild *Callimico goeldii* in northern Bolivia. *Neotrop. Primates* 16: 9–14.
- Gebo, D.L. 2011. Vertical clinging and leaping revisited: Vertical support use as the Ancestral Condition of Strepsirrhine primates. *Am. J. Phys. Anthropol.* 146: 323–335
- Kinzey, W.G., Rosenberger, A.L. and Ramirez, M. 1975. Vertical clinging and leaping in a neotropical primate. *Nature* 255: 327–328.
- Matauschek, C., Roos, C. and Heymann, E.W. 2011. Mitochondrial phylogeny of tamarins (*Saguinus*, Hoffmannsegg 1807) with taxonomic and biogeographic implications for the *S. nigricollis* species group. *Am. J. Phys. Anthropol.* 144: 564–574.
- Napier, J.R. and Walker, A.C. 1967. Vertical clinging and leaping, a newly recognised category of locomotor behaviour among Primates. *Folia Primatol.* 6: 204–219.
- Norconk, M.A. 1986. Interactions between primate species in a neotropical forest: mixed-species troops of *Saguinus mystax* and *S. fuscicollis* (Callitrichidae). Doctoral thesis, University of California, Los Angeles, California.
- Nyakatura, J.A. and Heymann, E.W. 2010. Effects of support size and orientation on symmetric gaits in free-ranging tamarins of Amazonian Peru: Implications for the functional significance of primate gait sequence patterns. *J. Hum. Evol.* 58: 242–251.
- Porter, L.M. 2001. Dietary differences among sympatric Callitrichinae in northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *Int. J. Primatol.* 22: 961–992.
- 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. and Garber, P.A. 2010. Mycophagy and its influence on habitat use and ranging patterns in *Callimico goeldii*. *Am. J. Phys. Anthropol.* 142: 468–475.
- Porter, L.M. and Garber, P.A. 2011. Foraging and spatial memory in saddleback tamarins (*Saguinus fuscicollis*). *Am. J. Phys. Anthropol.* 144 (Supplement 52): 242
- Rylands, A.B. 1996. Habitat and the evolution of social and reproductive behavior in Callitrichidae. *Am. J. Primatol.* 38: 5–18.
- Smith, R.J. and Jungers, W.L. 1997. Body mass in comparative primatology. *J. Hum. Evol.* 32: 523–559.
- Stafford, B.J., Rosenberger, A.L., Baker, A.J., Beck, B., Dietz, J. and Kleiman, D.G. 1996. Locomotion of golden lion tamarins (*Leontopithecus rosalia*): the effects of foraging adaptations and substrate characteristics on locomotor behavior. In: *Adaptive Radiations of Neotropical Primates*, M. Norconk, A.L. Rosenberger, and P.A. Garber (eds.), pp. 111–132. Plenum Press, New York.
- Walker, S.E. 1998. Fine-grained differences within positional categories: a case study of *Pithecia* and *Chiropotes*. In: *Primate Locomotion*, E. Strasser, J. Fleagle, A. Rosenberger, and H. McHenry (eds.), pp. 31–43. Plenum Press, New York.
- West, P.W. 2004. *Tree and Forest Measurement*. Springer Press, Berlin.
- 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.M. Ford, L.M. Porter, and L.C. Davis (eds.), pp. 279–297. Springer Press, New York.