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A Comparative Study of Positional Behavior in Three Species of Tamarin Monkeys

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ABSTRACT. Tamarins of the genus *Saguinus* are small-bodied New World monkeys that exhibit clawlike or modified nails. Patterns of positional behavior and habitat utilization are presented for three species, *Saguinus fuscicollis*, *S. geoffroy*, and *S. mystax*. These data were collected on free-ranging tamarin populations in Panama and Peru.

Despite considerable differences in body weight, all three species exhibited very similar patterns of positional behavior, with quadrupedal bounding and running accounting for 43–52% of travel time. Leaping was the second most common locomotor activity and accounted for 31–41% of travel. Although each species leaped principally on small supports in the perimeter of the tree crown, approximately 20% of all leaps in *S. fuscicollis* involved moderate to large sized vertical trunks located in the undercanopy. Leaping between trunks was rare in the two larger tamarin species.

Measurements taken on live wild-trapped adults reveal that compared to *Saguinus geoffroyi* and *S. mystax*, *S. fuscicollis* is characterized by a long legspan and an especially long armspan. It is proposed that in *S. fuscicollis*, elongated forelimbs play an important role in maneuvering and rotating the body during the in-air phase of trunk-to-trunk leaping, and increase the breaking distance needed to decelerate the body upon impact. Additional relationships between body size, substrate preference, and positional behavior in callitrichines are discussed.

Key Words: *Saguinus*; Tamarin; Positional behavior; Leaping.

INTRODUCTION

Tamarins of the genus *Saguinus* represent a successful radiation of 12 species of small-bodied New World primates that exhibit clawlike or modified nails on all manual and pedal digits excluding the hallux. Although there still exists considerable debate regarding the biological role of these specialized nails (HERSHKOVITZ, 1977; GARBER, 1980, in press; FORD, 1986), virtually all species studied are reported to cling to large vertical supports while feeding on resources such as plant exudates or insect prey. By embedding their elongated, laterally compressed, and pointed nails into the bark, these diminutive monkeys are able to exploit a set of arboreal supports that are otherwise too large to be grasped by their tiny hands and feet. Trunk foraging appears to be a primary adaptation in callitrichine primates, and serves to distinguish them ecologically from other Platyrrhine taxa (GARBER, in press b).

In contrast with studies on tamarin feeding ecology, there is little quantitative information on positional behavior during travel. Aspects of tamarin locomotion have been described as "springing" (ERIKSON, 1963), "squirrel-like climbing" (NAPIER & NAPIER, 1967), "rudimentary vertical clinging and leaping" (HERSHKOVITZ, 1977), "quadrupedal walking, running and bounding" (FLEAGLE & MITTERMEIER, 1980), and "acrobatic leaping in the periphery of the tree crown" (GARBER, 1980). Although these seemingly contradictory descriptions of tamarin position behavior may be explained by (1) species-specific differences in locomotor morphology and substrate preference, or (2) an overemphasis on certain spectacular but uncommon locomotor patterns, it is also possible that (3) the tamarin positional repertoire is extremely varied and includes a wide range of locomotor and postural behaviors on both very large and very small arboreal supports. In order to examine questions regarding locomotor adaptations in these New World primates, I present information on patterns of positional behavior and habitat utilization during travel in three species of callitrichines, *Saguinus fuscicollis* (saddle-back tamarin), *S. geoffroyi* (Panamanian tamarin), and *S. mystax* (Spix's moustached tamarin). These data were collected on free-ranging tamarins in Panama (*S. geoffroyi*, Rodman Field Site) and Peru (*S. mystax* and *S. fuscicollis*, Rio Blanco Field Site).

METHODS

Quantitative data on positional behavior were collected on habituated adult tamarins at 2-min (*S. mystax* and *S. fuscicollis*) or 2.5-min (*S. geoffroyi*) intervals throughout the day (focal animal point sampling technique; ALTMANN, 1974). Each instantaneous activity record included information on: (1) postural and locomotor behavior; (2) canopy level; (3) branch size (diameter); (4) branch orientation (with respect to the plane of the ground-horizontal, 0 – 15°; vertical, 75 – 90°; oblique, 16 – 74°); and (5) activity pattern.

Travel was defined as coordinated group movement or any nonforaging/nonpredator avoidance activity during which an individual crossed between the crowns of adjacent trees. Grasping refers to prehensile activities that occur on small supports. Clinging and scansorial locomotion are restricted to positional activities in which clawed digits are anchored into vertical or sharply inclined supports that are too large to be grasped.

Over 2,600 records of travel were recorded for each tamarin species. These samples were collected during all hours of the day and in both dry and wet seasons. A more detailed account of data collecting methods can be found in GARBER (1980, 1988).

Information on body weight, hand length, foot length, armspan, legspan, and head-body length was collected in the field on 102 live wild-trapped adult tamarins. Individuals were tranquilized with Ketamin Hcl and released after examination. Hand and foot measurements were made using a dial helios caliper (measurements taken to 0.01 mm); armspan, legspan, and head-body length were recorded using a measuring board (measurements taken to 0.1 mm). Interspecific differences in limb and body proportions were compared using the *t*-test. In order to insure that all individuals used in the analysis were of adult age, casts were made of the mandibular dentition of each tamarin. An individual was considered adult if all permanent dentition were in occlusion and there was evidence of wear on the premolars (GARBER & TEAFORD, 1986).

Measurements of tree height distributions and forest stratification were made in the home ranges of each of the study groups. In Panama, 23 transects, each 25 m in length and 1 m wide, were selected as sample plots from which to construct a profile of the Rodman forest. At the Rio Blanco Field Site in northeastern Peru, 200 5 m × 5 m quadrats were randomly selected for vegetation analysis. In both samples, all trees greater than 2 m in stature and 5 cm in circumference at breast height were measured and tallied.

At the Rio Blanco Field Site in northeastern Peru, moustached and saddle-back tamarins form mixed-species troops. Within such a troop, individuals of each species feed, forage, rest, travel together, and cooperatively defend a common home range throughout the entire year. Data on positional behavior in *S. mystax* and *S. fuscicollis* were collected on members of a single mixed species troop, and thus individuals of each species exploited a forest of identical structure and floristic composition.

RESULTS

FOREST PROFILES

The Rodman Field Site is a dry tropical forest located on the Pacific Slope of Panama (8°57′N, 79°57′W). This forest is composed principally of secondary vegetation and characterized by relatively few and widely scattered emergent trees surrounded by an irregular two-story canopy. Areas of well developed understory and edge vegetation are common. Over 74% of the 343 sample trees were 10 m or less in height and less than 10% exceeded 15 m (Fig. 1). Rainfall in this part of Panama averages 1,550 mm per year.

In Peru, moustached and saddle-back tamarins were studied at the Rio Blanco Field Site, a wet tropical forest (3,000 – 3,500 mm of rainfall per year) located approximately 110 km southeast of the city of Iquitos (4°05′S, 72°10′W). The home range of the study groups was characterized by a variety of habitat types including seasonally inundated forest, primary forest, secondary forest, and palm swamps. This Amazonian forest maintains a three-story canopy, with approximately 20% of the trees sampled greater than 15 m in height, and 3.4% estimated to reach heights of over 35 m (Fig. 1). The presence of a well developed main canopy creates an opportunity for continuous horizontal travel in the middle and upper stories of the forest. Tree density in the Peruvian forest was twice that recorded in the Panamanian forest (.38 trees/m^2 vs .19 trees/m^2).

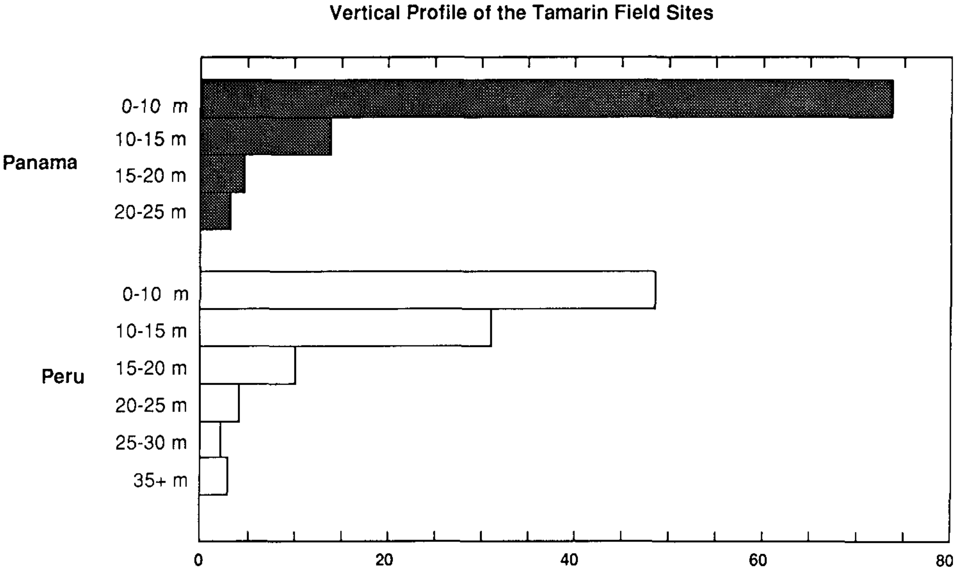

Fig. 1. Vertical height profile of the tamarin study sites (Rodman Research Site, Pacific Slope of Panama and Rio Blanco Research Site, northeastern Peru). *Saguinus geoffroyi* was studied at Rodman. *S. fuscicollis* and *S. mystax* were studied at the Rio Blanco.

POSITIONAL BEHAVIOR

Data on body weights in free-ranging adult tamarins are presented in Table 1. The three species studied represent the complete range of body sizes found among living tamarins.

Table 1. Adult body weights of wild-trapped tamarin monkeys.

Saguinus fuscicollis	300 – 400 g
S. oedipus	400 – 450 g
S. geoffroyi	450 – 525 g
S. labiatus	475 – 525 g
S. midas	450 – 550 g
S. mystax	525 – 650 g

S. fuscicollis is the smallest tamarin. Individuals of this species average between 300 – 400 g. *S. geoffroyi* represents the middle weight range at 450 – 525 g. *S. mystax* is reported to be the largest tamarin species. Adult body weight in Spix's moustached tamarin is approximately 525 – 650 g (Garber & Teaford, 1986; Snowdon & Soini, 1988). Despite these considerable differences in body weight each species exhibited a similar pattern of positional behavior, with quadrupedal walking, running, and bounding accounting for 43 – 52% of travel (Table 2). These locomotor activities tend to occur on moderate (6 – 10 cm in diameter) and large (>10 cm in diameter) supports in the lower and middle levels of the tree crown. Bounding differs from other forms of quadrupedal travel in that it includes both asymmetrical and symmetrical hindlimb dominated gaits, and is characterized by a brief in-air phase of stride. Bounding is a common locomotor pattern when tamarins ascend large obliquely oriented branches.

Leaping is the second most common locomotor activity and accounts for 31 – 41% of travel. Tamarins traverse both small and large gaps in the forest canopy by leaping. In each of the three species studied, terminal (≤5 cm in diameter) branches served as the landing platform in at least 55% of all leaps. Other modes of positional behavior occurred less frequently. Prehensile activities such as climbing and grasping accounted for 7 – 12% of travel. Claw-clinging and scansorial movements were observed 4 – 8% of the time.

A comparison of substrate size during travel failed to indicate any consistent relationship with body weight (Table 3). The largest and the smallest tamarin species, *S. mystax* and

Table 2. Positional behavior during travel in three species of tamarins.

	Positional category[1]				
Species	Quad	Climb/grasp	Leap	Cling/scans	Total
S. fuscicollis	1510 (47.6)	395 (12.4)	1033 (32.5)	201 (6.3)	3170
S. geoffroyi	1139 (43.3)	194 (7.4)	1090 (41.5)	204 (7.7)	2627
S. mystax	1729 (51.6)	418 (12.0)	1072 (30.9)	151 (4.3)	3468

1) Quad: Quadrupedal progression such as walking, running, and bounding; Climb/grasp: includes a variety of prehensile climbing activities and grasping postures; Leap: includes acrobatic leaps, bounding leaps, and leaping to and/ or from vertical trunks (see text for descriptions); Cling/scans: includes claw-clinging and scansorial travel on large vertical or sharply inclined supports. Percentage in parentheses.

Table 3. Patterns of support preference during travel in three tamarin species.

	Support size (diameter in cm)			
Species	0 – 5	>5 – 10	>10	Total
S. fuscicollis	1062 (33.9)	888 (28.3)	1180 (37.5)	3130
S. geoffroyi	1483 (49.0)	753 (24.9)	791 (26.0)	3027
S. mystax	1202 (35.2)	899 (26.4)	1305 (38.2)	3406

Percentage in parentheses.

S. fuscicollis exhibited the same overall pattern of substrate preference, utilizing larger and smaller supports more frequently than moderate sized supports. In contrast, the Panamanian tamarin showed a clear preference in traveling on the smallest branches. In this species fragile supports accounted for almost 50% of the travel, whereas moderate and large supports were each utilized approximately 25% of the time.

During travel, tamarins exhibit three forms of leaping behavior.

Acrobatic Leap

These are long leaps (usually 5 m or greater) which are used to cross large gaps in the upper canopy or to move between the crowns of adjacent trees. Such leaps typically begin and end on a mass of terminal supports in the outer margins of the tree crown. The tail is used as a counter-balance to slow the rate of descent, and the forelimbs strike the landing platform in advance of the hindlimbs. In the majority of cases, strong hindlimb propulsion is not required to produce an effective downward leap.

Bounding Leap

These are short leaps of less than 2 m. They are an outgrowth of rapid quadrupedal progression and are used by the tamarins when crossing between two large but discontinuous arboreal supports. The bounding leap differs from bounding or quadrupedal running in its substantially longer in-air phase of stride and increased hindlimb extension in order to produce a greater propulsive thrust.

Trunk-to-trunk Leaping

These are leaps of usually 1 – 2 m that begin and end on moderate-to-large trunks in the undercanopy. Due to the brief nature of the jump, there is only minimal height loss in moving from the takeoff to the landing platform. Force generated to produce the leap is provided by powerful hindlimb extension. The forelimbs strike the landing surface in advance of the hindlimbs and are abducted. Trunk-to-trunk leaping differs from most other forms of travel in that the jump originates out of a stationary posture, the animal is facing away from the landing platform and must quickly rotate its body while airborne, and immediately after landing the body comes to a state of rest. In tamarins, movement between trunks is rarely rapid or sequential as is reported in certain Malagasy and African prosimians. Rather, these small monkeys cling for a period of time and survey the surrounding vegetation before leaping to another trunk or arboreal support.

These three modes of leaping occur in different parts of the canopy and are associated with supports of different sizes and orientations. A comparison of their frequency in *S. fuscicollis*, *S. geoffroyi*, and *S. mystax* is presented in Table 4. Although leaping occurs principally on small supports in the perimeter of the tree crown (acrobatic leaping), in the smallest tamarin species, *S. fuscicollis*, 19.2% of all leaps were between tree trunks located in the undercanopy. In an additional 7.3% of leaps, trunks served only as a landing platform. In comparison, trunk-to-trunk travel accounted for 8.8% of leaping in the moustached tamarin, and only 3.8% in the Panamanian tamarin. In this latter species three-fourths of all leaps were long acrobatic jumps, and 17% were bounding leaps. This high proportion of acrobatic leaps to bounding leaps in *S. geoffroyi* may reflect a behavioral response to traveling in an extremely discontinuous canopy. In both of the

Table 4. Leaping behavior during travel in three species of tamarins.

	Modes of leaping			
Species	Acrobatic	Bounding	Trunk-trunk[1]	Total
S. fuscicollis	557 (55.3)	184 (18.2)	194 (19.2)	1008
S. geoffroyi	813 (74.5)	185 (16.9)	42 (3.8)	1090
S. mystax	686 (64.6)	258 (24.3)	94 (8.8)	1061

1) *S. fuscicollis*: In an additional 73 (7.3%) leaps, trunks served only as a landing platform; *S. geoffroyi*: in an additional 20 (1.8%) leaps, trunks served only as a landing platform; *S. mystax*: in an additional 23 (2.2%) of leaps, trunks served only as a landing platform. Percentage in parentheses.

Amazonian species, movement between tree crowns commonly involved quadrupedal progression (Table 2) or short bounding leaps (Table 4).

Despite its small body weight, *S. fuscicollis* leaps to-and-from large vertical supports in the undercanopy more frequently than either *S. geoffroyi* or *S. mystax*. Are there indications that differences in positional behavior and substrate preference are associated with modifications of the locomotor skeleton?

Evidence based on measurements of body weight, armspan, legspan, hand length, foot length, and head-body length taken on live adult wild-trapped tamarins reveals significant interspecific differences in skeletal proportions. When corrected for body mass (length divided by weight $^{.33}$), armspan and legspan scale negatively allometric in the three tamarin species studied (Table 5). The smallest species, *Saguinus fuscicollis* has a significantly longer armspan ($t=5.06$, $p<.001$ comparison with *S. geoffroyi* and $t=9.97$, $p<.001$ comparison with *S. mystax*) and legspan ($t=2.9$, $p<.005$ comparison with *S. geoffroyi* and $t=6.2$, $p<.001$ comparison with *S. mystax*) than either of its larger-bodied congeners. Relative armspan ($t=3.46$, $p<.005$) and legspan ($t=2.75$, $p<.009$) in *S. geoffroyi* are longer than that found in the largest tamarin species, *S. mystax*.

Table 5. Allometrically corrected measures of head-body, forelimb, and hindlimb length in three species of tamarins.

	Allometrically corrected values[1]					
Species	Head-body length	Hand length	Foot length	Armspan	Legspan	AS/LS (×100)
S. fuscicollis ($N=47$)						
Mean values	31.5	6.1	9.1	43.8	50.2	87.6
S.D.	1.5	0.2	0.3	1.8	2.1	0.03
S. geoffroyi ($N=21$)						
Mean values	30.2	5.9	8.6	41.3	48.6	85.0
S.D.	0.9	0.3	0.4	1.5	1.6	0.03
S. mystax ($N=34$)						
Mean values	31.6	5.7	8.5	39.5	46.5	84.9
S.D.	1.0	0.2	0.4	1.9	2.9	0.03

1) Values were calculated separately for each individual by dividing the length of its limb segments by its body weight raised to the .33 power. Species means and standard deviations were then compiled. Head-body length: Measured from the crown of the head (mid-parietal region) to the distal part of the ischium; Hand length: measured from the carpus to the terminal phalanx of the longest digit (digit 3); Foot length: measured from the calcaneous to the terminal phalanx of the longest digit (digit 3); Armspan: with the arms extended, supinated, and abducted, a measure of the distance from the terminal phalanx of the longest digit of the right hand to the terminal phalanx of the longest digit of the left hand; Legspan: with the legs extended and abducted, a measure of the distance from the terminal phalanx of the longest digits of the right foot to the terminal phalanx of the longest digit of the left foot.

In contrast, hand and foot length do not follow this same pattern. Although *S. fuscicollis* has longer hands and feet than *S. geoffroyi* ($t=2.62$, $p<.02$ and $t=4.42$, $p<.001$) and *S. mystax* ($t=6.53$, $p<.001$ and $t=7.50$, $p<.001$), relative to body weight these latter two species do not differ in these measures (hand length, $t=1.9$, $p>.05$; foot length, $t=1.5$, $p>.05$; Table 5).

An index of limb proportions, or the ratio of armspan to legspan (AS/LS × 100), provides additional insight into differences in tamarin skeletal morphology. A comparison between the three species indicates that the AS/LS ratio in the saddle-back tamarin (87.6) is higher ($p<.005$) than that recorded for either the Panamanian (85) or moustached tamarin (84.9). Despite large differences in body weight and absolute limb length, the ratio of armspan to legspan in *S. geoffroyi* and *S. mystax* is identical ($t=0.02$, $p=.98$). These data suggest that *S. fuscicollis* is not only a long-limbed tamarin, but that when compared with the other tamarins, it is the forelimbs that are especially elongated relative to the hindlimbs.

DISCUSSION

A number of theories have been proposed to account for the loss of digital claws in primate evolution. It has been argued that claws are less effective than nails in locomoting on thin terminal supports (Hershkovitz, 1977; Cartmill, 1974; Szalay & Dagosto, 1980) and a functional disadvantage in jumping between vertical trunks (Szalay, 1972). Field data presented on positional behavior in three species of tamarin monkeys do not support these contentions. Tamarins range through all zones of the forest canopy and travel on supports of all sizes and orientations. In relationship to their body size, these primates exhibit a remarkable range of locomotor plasticity, exploiting arboreal supports of both very large and very small diameters. Patterns of positional behavior are closely associated with branch size and orientation. For example, on thin fragile supports callitrichine locomotion is characterized by climbing, jumping, and other prehensile activities. Although tamarins have a reduced hallux (as do many other New World primates), hallucial adduction serves an important grasping function.

In contrast, when locomoting on supports in excess of 10 cm in diameter, grasping and prehensile activities are less effective and replaced by quadrupedal walking, running, and bounding locomotion. Supports of this size are large relative to tamarin body and limb size and provide a fairly stable base of support during travel. On large vertical or sharply inclined branches such as tree trunks, tamarins exhibit a noticeable change in positional repertoire and embed their clawlike nails into the bark to maintain support. Although trunk-to-trunk leaping has been reported in many tamarin species (*S. imperator*, Terborgh, 1983; *S. midas*, Thorington, 1968; *S. labiatus*, Pook & Pook, 1982; *S. geoffroyi & S. mystax*, this paper), only in *S. fuscicollis* does it appear to be a common and dominant mode of locomotion (Moynihan, 1976; Crandlemire-Sacco, 1986; Norconk, 1986; Soini, 1987).

Cartmill (1974, 1979, 1985) has argued that clawed or claw-like digits are superior to clawless digits when traveling on large trunks. By anchoring their claws into the bark an animal can effectively decrease the angle at which its limbs contact the trunk and thereby reduce the adduction force needed to maintain support. In this regard, when clinging to or locomoting on large diameter trunks, small clawed animals with shorter limbs are not expected to be disadvantaged over small clawed animals with longer limbs. This is supported by field observations and body measurements taken on tropical sciurids (sciurids often use the trunk or central axis of the tree in ranging vertical through the crown; Garber &

SUSSMAN, 1984). Data collected by EMMONS (1975) on nine species of squirrels in Gabon fail to indicate any consistent differences in intermembral index, forelimb length (humerus + radius), or hindlimb length (femur + tibia) associated with body size or degree of arboreal and terrestrial locomotion. In general, arboreal nongliding sciurids do not have longer forelimbs or hindlimbs than their more terrestrial relatives (THORINGTON & HEANEY, 1981).

The question remains, why does *Saguinus fuscicollis* have relatively long hindlimbs and especially long forelimbs when compared to other tamarins such as *S. geoffroyi* and *S. mystax*. Two explanations are offered. The first relates to allometry and a pattern of dwarfing in which decreases in body weight proceed at a greater rate than decreases in limb length. Using data on body weight and limb measurements collected from the same individuals there is evidence that, in contrast with most primate taxa, both armspan and legspan scale negatively allometric in the three tamarin species studied. This pattern does not appear to be true of callitrichines in general, however. In his examination of limb proportions in six species of *Callithrix*, *Leontopithecus*, *Saguinus*, and *Cebuella*, JUNGERS (1985) found that both fore- and hindlimbs were positively allometric, "with the hindlimb exponent slightly greater than that of the forelimb." Given these findings larger-bodied callitrichines are expected to exhibit lower intermembral indices than smaller-bodied callitrichines. A comparison of intermembral indices among 11 tamarin and marmoset species (indices and body weight data complied from HERSHKOVITZ, 1977; FLEAGLE, 1988; SNOWDON & SOINI, 1988; GARBER, in press b), however, fails to indicate any consistent relationship with body weight (Fig. 2, $r = -0.29$, $p > 05$). Thus, it is unlikely that species-specific differences in callitrichine limb proportions are principally size dependent.

An alternative explanation for limb elongation in the saddle-back tamarin is related to the frequency with which this species leaps to-and-from large trunks in the forest understory. As noted earlier, trunk-to-trunk leaping differs from other forms of locomotion in that (1) the leap begins from a stationary clinging posture and therefore the animal must overcome a significant degree of inertia, and (2) since the animal is not facing the landing substrate during takeoff, the body must be rotated almost 180° while airborne. Given that the muscular force used in these leaps is hindlimb generated, long and/or muscular hindlimb segments can increase the velocity at takeoff and the distance the animal can be propelled in order to reach its target support (EMERSON, 1985). This interpretation is consistent with the observation that among the prosimians, "small vertical clingers and leapers have relatively longer hindlimbs than do nonjumpers of the same body size" (EMERSON, 1985). Similarly among New World primates of the subfamily Pitheciinae, *Pithecia pithecia* a frequent leaper (70% of travel) has elongated hindlimbs when compared with *Chiropotes satanas*. This latter species is principally quadrupedal, with leaping accounting for only 18% of travel (FLEAGLE & MELDRUM, 1988).

A second problem faced by trunk-to-trunk leapers involves the in-air body rotation needed to bring the limbs in position for landing. Such rotation must be accomplished without the aid of any externally applied force (DUNBAR, 1988). When leaping to a vertical trunk, many of the smaller bodied leapers such as the Bornean tarsier (*Tarsier bancanus*), lesser galago (*Galago senegalensis*), sportive lemur (*Lepilemur mustelinus*), and ring-tailed lemur (*Lemur catta*) land on their hindlimbs (HALL-CRAGGS, 1965; WALKER, 1979; NIEMITZ, 1984; PETERS & PREUSCHOFT, 1984; DUNBAR, 1988; DEMES & GUNTHER, 1989). In these species, twisting of the body along its longitudinal axis and displacement of the hindlimbs anterior to the body is accomplished principally by adjustments in the position and movement of the tail (PETERS & PREUSCHOFT, 1984; DUNBAR, 1988). The forelimbs contribute

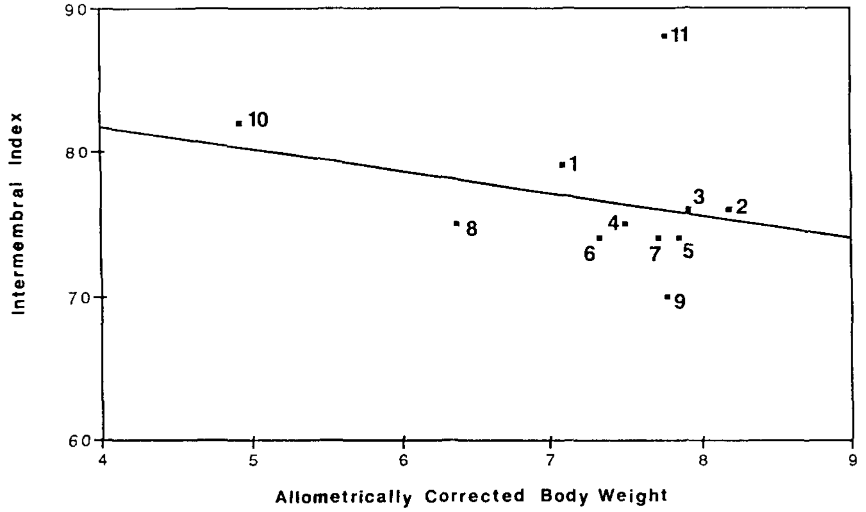

Fig 2. Relationship between body weight (weight $^{.33}$) and intermembral index in 11 species of callitrichines. 1=*Saguinus fuscicollis*; 2=*S. mystax*; 3=*S. labiatus*; 4=*S. imperator*; 5=*S. midas*; 6=*S. oedipus*; 7=*S. leucopus*; 8=*Callithrix jacchus*; 9=*Callimico goeldii*; 10=*Cebuella pygmaea*; 11=*Leontopithecus rosalia*.

little to accelerating, rotating, or slowing down the body when jumping between vertical supports.

In contrast, saddle-back tamarins adopt a very different pattern of body orientation and landing during trunk-to-trunk leaping. Throughout the airborne phase of the leap, the body is oriented in a horizontal or diagonal plane, with the forelimbs positioned well in advance of the hindlimbs. In this posture, the animal's center of gravity is directed forward, allowing the forelimbs to strike the trunk first and sustain most of the compressive loads generated upon impact. Repositioning and rapid movements of their long arms while airborne may play an important role in initiating body rotation prior to landing. In addition, elongated forelimbs provide an advantage in increasing the breaking distance needed to decelerate the body when landing on the trunk (PETERS & PREUSCHOFT, 1984). Filmed sequences and biomechanical analyses of trunk-to-trunk leaping in *S. fuscicollis* and other callitrichines are needed in order to determine more precisely the role of the forelimbs in maneuvering and decelerating the body during leaping.

During certain periods of the year, both the Panamanian tamarin and the moustached tamarin spend considerable amounts of time clinging to trunks while feeding on plant exudates (GARBER, 1980, 1984, in press a; NORCONK, 1986). As indicated in this study, however, these species rarely leap between trunks. In *S. geoffroyi* and *S. mystax* trunks are used as landing platforms in less than 3.5% of total travel. Thus, although clawed digits enable small, long- or short-armed monkeys to adopt a variety of stable clinging postures, clawed digits alone may not provide the necessary mechanical advantage required when leaping between large vertical trunks. This is consistent with KINZEY et al.'s (1975) contention that among callitrichines "claws...are for clinging to large vertical supports, and are not part of a complex related to leaping."

Two additional points are worth noting. The first is that keeled or clawlike nails have evolved independently in a number of primate lineages including callitrichines, *Dauben-*

tonia madagascariensis, *Tarsius pumilus*, *Phaner furcifer*, and *Euoticus elegantulus*. In virtually all cases, these specialized digits appear to be associated with the exploitation of resources extracted from trunks and other large vertical supports rather than as an adaptation to travel. For example, in his detailed study of prosimian locomotion, CHARLES-DOMINIQUE (1977) describes travel in *Euoticus* as "reminiscent of the cercopithecine monkeys." This species, however, commonly clings to large vertical supports when feeding on plant exudates. Similarly, the locomotor behavior of *Daubentonia* and *Phaner furcifer* is described as quadrupedal running and jumping, with little mention of leaping between large vertical trunks (although such supports are occasionally used as a landing platform, PETTER et al., 1975; TATTERSAL, 1982). These prosimians are trunk foragers, however, and exploit wood-boring insects, insect galls, and/or exudates (POLLOCK et al., 1985). Neither the aye-aye nor the forked-tooth lemur have relatively long forelimbs for a prosimian of their body size (JUNGARS, 1985).

The second point involves the relationship between body size, use of vertical supports, and hindfoot adaptations in primates. In examining the musculo-skeletal anatomy of prosimians, GEBO (1985) identified two contrasting pedal grasping patterns, a nonpowerful I – V opposable grasp which characterizes the cheirogaleids, lorisids, tarsiids, and *Daubentonia*, and a derived powerful I – II adductor grasp which is unique to the lemurids and indriids. He notes that all of the prosimian vertical clingers under 250 g utilize the I – V grip whereas all of the vertical clingers over 500 g exhibit the I – II power grip. "Between 250 – 500 g there are no vertical clinging species (GEBO, 1985). Given that callitrichines retain a I – V opposable pedal grasp and virtually all extant species fall within this 250 – 500 g weight range, the evolution of clawlike nails in this lineage may represent a solution to what GEBO (1985) has termed a "weight threshold problem" enabling tamarins and marmosets to adopt a stable clinging posture on relatively large vertical substrates.

Additional detailed information on positional behavior and morphology in callitrichines is needed in order to examine more fully relationships between fore- and hindlimb anatomy, body weight, and patterns of habitat utilization. In particular, studies of Goeldi's monkey (*Callimico goeldii*), the pygmy marmoset (*Cebuella pygmaea*), the pied tamarin (*Saguinus bicolor*), and the black-mantle tamarin (*S. nigricollis*), all reportedly trunk-to-trunk leaping species [note, however, that SOINI (1988) has suggested that leaping between large trunks is not a common part of the locomotor repertoire of *Cebuella pygmaea*] are critical for testing and evaluating form, function, and ecological relationships associated with claw-clinging and leaping in this important New World primate subfamily.

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