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RESEARCH ARTICLE

Leaping Behavior of *Pithecia pithecia* and *Chiropotes satanas* in Eastern Venezuela

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I observed leaping behavior in the white-faced saki (*Pithecia pithecia*) and the black-bearded saki (*Chiropotes satanas satanas*) for 15 and 10 months, respectively, as part of a larger study of positional behavior in the tribe Pitheciini. I used focal animal instantaneous sampling to observe the two species on separate islands in their natural habitat at Guri Lake, Venezuela. Leaping behavior correlates with patterns of forest use and body size, and differences between the species relate more to habitat preferences than to habitat differences per se. *Pithecia* usually chose vertical or highly angled supports of lower tree portions for take-off and landing, and took off from a stationary posture. *Chiropotes* took off from the main crown or terminal branches, gaining momentum from locomotor movement before performing a leaping take-off. *Pithecia*'s vertical body orientation and longer leap distance allowed it to assume a mid-flight tuck to prepare for a hindlimb-first landing onto a solid support, and to absorb landing forces with its relatively longer hindlimbs. *Chiropotes* remained more pronograde throughout its leaps, and minimized landing forces by landing on all four limbs onto numerous flexible supports in the terminal branches. The smaller-bodied *P. pithecia* is specialized for vertical clinging and leaping, and exhibits behavioral and morphological parallels with other vertical clingers and leapers. The larger *C. satanas* is a generalized leaper that lacks morphological specializations for leaping. *Pithecia*'s use of solid supports in the lower tree portions allows it to move quietly through the forest–one of a suite of behaviors related to predator avoidance. This example of variation within one behavioral category has implications for devising locomotor classifications and interpreting fossil remains. Am. J. Primatol. 66:369–387, 2005. © 2005 Wiley-Liss, Inc.

Key words: primate leaping; Pitheciinae; positional behavior

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INTRODUCTION

Primate leaping has been the subject of study in a diverse range of primates, but most often with a focus on the vertical clinging and leaping of prosimians [e.g., Burr et al., 1982; Demes et al., 1996; Grand & Lorenz, 1968; Napier & Walker, 1967; Niemitz, 1983; Peters & Preuschoft, 1984]. Leaping is an important component of the locomotor repertoire because it plays a key role in predator avoidance [Crompton, 1984; Gebo et al., 1994; Walker, 1993b] and in crossing gaps in the forest matrix [Cannon & Leighton, 1994; Cant, 1988]. It is also of particular interest because it provides an example of a single behavioral category in which the behavioral and morphological characteristics differ among various species [Anemone, 1990; Demes & Günther, 1989; Fleagle & Meldrum, 1988; Oxnard et al., 1981; Walker, 1993a], thus illuminating potential methodological and interpretational problems with traditional classifications of locomotor behavior.

As with all positional behaviors, leaping is influenced by various phylogenetic and ecological factors. By studying members of a monophyletic group, one can investigate certain evolutionary issues, such as separating the effects of past evolutionary history from more recent environmental pressures. The tribe Pitheciini, which is comprised of the genera *Pithecia*, *Chiropotes*, and *Cacajao*, provides a useful subject for such studies. Anatomical and molecular evidence supports the notion of closer affinities between *Chiropotes* and *Cacajao* than with either of these to *Pithecia* [Boubli & Ditchfield, 2000; Kinzey, 1992; Rosenberger, 1988].

The importance of leaping in *Pithecia* and quadrupedalism in *Chiropotes* was previously documented [Fleagle & Mittermeier, 1980], but long-term field studies of their positional behavior have been lacking. This paper draws from the first such study on pitheciin positional behavior to focus on leaping behavior and associated support use in the white-faced saki (*Pithecia pithecia*) and black-bearded saki (*Chiropotes satanas satanas*) to more closely examine interspecific differences and the influence of habitat, body size, and morphology. Also considered are the biomechanical advantages of particular behaviors, the function of primate leaping, and the implications of variation in behavioral categories for establishing and using locomotor classifications.

MATERIALS AND METHODS

Study Site and Study Species

I conducted observations of wild groups of *P. pithecia* and *C. s. satanas* (henceforth referred to as *Pithecia* and *Chiropotes*) at Guri Lake (7.30°N, 63.00°W) in eastern Venezuela (Fig. 1), between October 1989 and May 1991. This 4,300 km^2 lake was created in 1968 when the Caroni River Basin was flooded after the construction of the Raul Leoni dam. The inundation created numerous forested islands, three of which comprise the study site (referred to here as the "*Pithecia*" and "*Chiropotes*" islands). The islands' vegetation is quite similar to that of the Caroni Basin before it was flooded [Pernía, unpublished results] (L. Balbás, personal communication).

Pithecia and *Chiropotes* are largely sympatric in the Guayanas, but occur only allopatrically in Venezuela [Bodini & Perez-Hernández, 1987; Kinzey et al., 1988], separated by the Caroni River. In Guri Lake, *Pithecia* and *Chiropotes* inhabit islands (formerly forests on opposite sides of the Caroni River) that are approximately 45 km apart. Two *Pithecia* groups were studied on separate

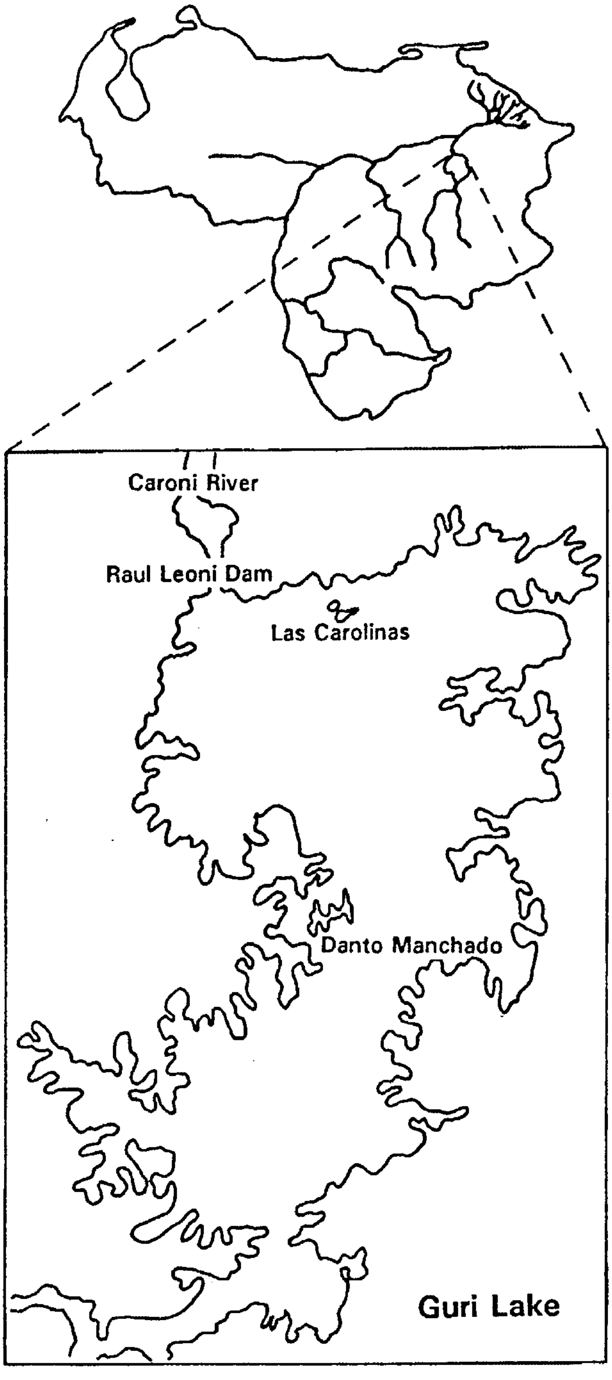

Fig. 1. Map of Venezuela with inset of Guri Lake.

islands: one group consisted of eight individuals (three adult males, three adult females, one juvenile, and one infant), and one group consisted of two females (after the group male disappeared). The single *Chiropotes* group numbered 18–20 individuals (including one adult male, several adult females, and young of various ages). *Pithecia* is the smaller species, with males and females weighing approximately 1.8 kg and 1.4 kg, respectively. *Chiropotes* males and females weigh about 3 kg and 2.6 kg, respectively [Ford & Davis, 1992], and sexual dimorphism in *P. pithecia* and *C. satanas* is 81% and 86%, respectively.

Data Collection

I collected data using instantaneous sampling on a focal animal at 2-min intervals, observing an individual until it disappeared from view for 5 min. I then chose another focal animal. The difficulties of collecting and analyzing data in positional behavior studies have been widely discussed [Cant, 1988; Dagosto, 1994; Doran, 1992; Hunt, 1992; Hunt et al., 1996; Mendel, 1976; Walker, 1996]. Doran [1992] found that focal animal and bout sampling yielded highly similar results, although behaviors that occurred as a brief point in time (events) were underrepresented. In an on-site pilot study that was conducted before the actual data collection began, I combined focal-animal sampling with bout sampling, and achieved results similar to those of Doran. Since gap-crossing behaviors are events, I dealt with the potential bias by slightly expanding the window of sampling around a focal point. That is, if a gap-crossing behavior occurred within 5 sec of a sample point, that was the behavior recorded. I collected approximately equal amounts of data for males and females, and used only data from adults for this analysis. Comparisons using chi-square analysis did not reveal significant differences in leaping behavior between the sexes. *Pithecia* males and females are easily distinguished by their sexual dichromatism. Such differences are most extreme in *P. pithecia*: males have black body fur and white faces, and females have agouti-colored fur except for their yellow-gold ventrum, forehead, and maxillary region [Hershkovitz, 1979]. *Chiropotes* males and females are more difficult to distinguish, but the males' larger body size and often-visible large pink scrotum usually make identification possible. I recorded approximately 50 hr of observations per month for each species, resulting in 939 leaps analyzed for *Pithecia* (over 15 months) and 420 for *Chiropotes* (over 10 months).

The data presented here are limited to leaping behavior, and represent part of a larger data set on positional behavior and habitat characteristics [Walker, 1992, 1993b, 1996]. Leaping and other gap-crossing behaviors are defined in Table I. Most of the take-off positions observed in these primates (quadrupedal walk, quadrupedal run, vertical cling, and stand) are now standard and have been defined similarly in various studies [e.g., Ripley, 1977; Rose, 1979]. The exceptions (pronograde clamber, pronograde clamber-run, and climb) are defined in Table I. I collected data on the following variables for each leap sample recorded: the height of the animal and its supporting tree at take-off, tree portion (lower tree portions, main crown, terminal branches, and lianas), and support characteristics. The support characteristics included the number of supports (one, two, or several), support inclination (horizontal: 0–20°; angled either upward or downward relative to the animal's orientation: 20–70°; vertical: 70–90°; deformable if support deformed under animal's body weight at take-off or landing; or mixed if supports of various angles were combined), and support diameter (<2 cm, 2–5 cm, 6–10 cm, 11–15 cm, >15 cm, and mixed if supports of various diameters were combined).

I videotaped the primates with a Sony Handycam CCD-V99 high-resolution 8-mm camcorder. The still-frame feature proved helpful for categorizing

TABLE I. Gap-Crossing Behaviors and Take-Off Positions

Gap-crossing behaviors

- Leap: means of rapid progression between discontinuous supports, involve simultaneous hindlimb extension to provide propulsive thrust [Emerson, 1985]. Following parabolic trajectory, the animal is displaced horizontally, sometimes with downward component.
- Drop: used to cross vertical gaps in the canopy, and involve primarily vertical displacements with little or no horizontal component. Hindlimbs used only minimally in propulsion (evidenced by low degree of hindlimb flexion preceding take-off). Trunk tends to be oriented horizontally when dropping onto flexible supports, and angled down when dropping onto rigid supports.
- Hop: little displacement occurs between take-off and landing, each stage short in duration and distance covered. Forelimbs play little or no role in take-off or landing. Generally performed within a tree to cross a small gap, or used along a branch.
- Continuous leap: used only by *Pithecia* for rapid movement. Several consecutive leaps are exhibited, usually initiated from a vertical cling position. Landings are hindlimb-first onto solid support; hindlimbs are immediately extended to initiate the next leap.

Take-off positions

- Pronograde clamber [Cant, 1988]: locomotion across multiple substrates in horizontal or diagonal direction. Use of multiple substrates that are often of various sizes, inclinations, and orientations results in an irregular gait, characterized by abducted and flexed limbs, which lower the center of gravity. Typically used in the terminal branches.
- Pronograde clamber-run [Walker, 1993b]: Similar to Cant's [1988] pronograde clamber in terms of supports used, but with a faster gait.
- Climb: Locomotion on supports with steeply sloping surfaces as in Rose [1979] and Cartmill [1985].

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positional behaviors by allowing detailed observations of limb positions, and for analyzing qualitative differences between the species' leaps.

I estimated the heights and support diameters by eye after practicing for approximately 2 months by comparing clinometer results with my height estimates, and diameter at breast height (DBH) tape measurements with my diameter estimates. While the limitations in field methodology must be acknowledged, I obtained a high degree of accuracy after the practice period was completed.

Data Analysis and Presentation of Results

I used the chi-square test to analyze the overall differences between *Pithecia* and *Chiropotes* in leaping behavior and support use. Differences were considered significant if the associated probability of the chi-square statistic was less than .01. Quantitative data are presented for take-off positions, relative heights of leaps, and tree portions and supports used. The qualitative aspects compared between species were body orientation, landing positions, and leap distance.

RESULTS

The overall frequencies of gap-crossing behaviors compared to other forms of locomotion are presented in Table II. These behaviors contributed considerably to the overall difference in locomotion between the species ($\chi^2=553.01$, $P<0.001$). *Pithecia* leapt considerably more than *Chiropotes*, but dropped less. Hopping was

TABLE II. Gap-Crossing Behaviors Compared to Other Forms of Locomotion

	Pithecia (n=2944)	*Chiropotes* (n=1818)
Gap-crossing behaviors	45.6%	33.2%
Leap	39.7	24.5
Drop	1.1	7.6
Hop	1.8	1.1
Continuous leap	3.0	0
Other locomotion	54.4	66.8
Total	100	100

TABLE III. Take-Off Positions for Leaping

	Pithecia (n=939)	*Chiropotes* (n=420)
Locomotor positions	36.3%	76.2%
Pronograde clamber	12.9	33.1
Quadrupedal walk	14.1	23.1
Quadrupedal run	8.3	18.3
Pronograde clamber-run	–	1.7
Climb	1.0	–
Postures	63.2	22.9
Vertical cling	51.3	–
Stand	11.9	22.9
Other	0.5	1.0
Total	100.0	100.1

little used by either species, and continuous leaping was observed only in *Pithecia*, although infrequently.

Leap Take-Off Positions

Pithecia frequently used a stationary posture for take-off, while *Chiropotes* more often took off from a locomotor position (Table III). The species differed in take-off positions ($\chi^2=340.04$, $P<0.001$), with vertical cling and pronograde clamber being the most frequently used positions for *Pithecia* and *Chiropotes*, respectively. Quadrupedal walking and running for take-off were used more frequently by *Chiropotes* than by *Pithecia*. The only posture that was used more for take-offs by *Chiropotes* compared to *Pithecia* was standing.

Leap Landing Positions

I did not collect quantitative data on leap landing positions; however, a brief description for each species is provided here: *Pithecia* typically landed hindlimb-first, which was particularly apparent in longer leaps. For shorter leaps, all four limbs sometimes struck the landing substrate at the same time, or the forelimbs contacted slightly before the hindlimbs. In *Chiropotes*, all four limbs typically encountered the substrate at the same time; in very short leaps, the forelimbs sometimes struck first. The degree of limb abduction at landing depended on the support type used, with more abduction used when the animal landed on a network of flexible branches.

Leaping and Relative Height in Trees

Relative height is expressed as a percentage of the animal's height in the tree relative to the tree's height. A comparison of relative tree heights used by leaping *Pithecia* and *Chiropotes* is shown in Table IV (χ^2=92.59, $P<0.001$). The two uppermost height categories (90–100% and 80–90%) were used less by *Pithecia* than by *Chiropotes*. The next category (70–80%) was used approximately equally by both species, and the lower height categories were used more by *Pithecia*.

Tree Portions Used in Take-Off and Landing

Take-off.

Tree portions used for take-off differed greatly between the species (χ^2=338.82, $P<0.001$; Table V). *Pithecia* used lower tree portions (vertical axis, below crown, and bole) in over one-half of their sampled leaps, while *Chiropotes* rarely used these portions. The most important take-off portions for *Chiropotes* were the crown and the terminal branches. While *Pithecia* also commonly used the crown for take-off, they seldom used the terminal branches. Liana use was higher for *Pithecia* than for *Chiropotes*.

TABLE IV. Leaping and Relative Height in Trees

Relative height in tree (% of tree height)	*Pithecia* (n=816)	*Chiropotes* (n=441)
90–100%	2.3	7.7
80–90	16.4	32.9
70–80	32.1	33.3
60–70	24.6	15.4
50–60	16.7	8.2
40–50	4.8	1.6
<40	3.2	1.0
Total	100.1	100.1

TABLE V. Tree Portions Used in Take-Off and Landing

	Take-off		Landing	
Tree portion	*Pithecia* (n=879)	*Chiropotes* (n=408)	*Pithecia* (n=647)	*Chiropotes* (n=227)
Main crown	33.2%	46.1%	16.1%	5.7%
Terminal branches	10.0	44.6	20.6	88.1
Vertical axis	10.1	0	11.6	0
Below crown	10.7	5.6	11.3	3.1
Bole	30.6	0	35.1	0
Liana	5.4	2.5	5.4	2.6
Total	100	98.8	100.1	99.5

Landing.

Tree portions used in landing also differed significantly between the species ($\chi^2 = 333.40$, $P < 0.001$; Table V). *Pithecia* most frequently landed in the lower tree portions, which were seldom used by *Chiropotes*. *Pithecia* used the main crown for landings more than did *Chiropotes*, while terminal branches were by far the preferred landing site for *Chiropotes*. Liana use for landings was similar to that of take-off, with greater use exhibited by *Pithecia*.

Number of Supports Used in Take-Off and Landing

Take-off.

Significant differences were observed in the number of take-off supports used ($\chi^2 = 108.55$, $P < 0.001$; Table VI). Both *Pithecia* and *Chiropotes* took off from a single support in the majority of their leaps, with *Pithecia* using single supports more than did *Chiropotes*. Two (dual) supports were little used in take-offs by either species, while several supports were used much more by *Chiropotes* than by *Pithecia*.

Landing.

Differences in the number of landing supports used by the two species were greater than those for take-off supports ($\chi^2 = 235.27$, $P < 0.001$). More *Pithecia* than *Chiropotes* landings were made onto a single support. Dual supports were seldom used by either species. *Chiropotes* most often landed on several supports, which were much less frequently used by *Pithecia* for landing.

TABLE VI. Supports Used in Take-Off and Landing

	Take-off		Landing	
	Pithecia	Chiropotes	Pithecia	Chiropotes
Number of supports	(n=896)	(n=407)	(n=824)	(n=366)
One	85.0%	60.7%	84.3%	41.3%
Two	4.1	4.7	1.7	2.5
Several	10.8	34.6	14.0	56.3
Total	99.9	100	100	100.1
Inclination	(n=892)	(n=408)	(n=828)	(n=367)
Horizontal (0–20°)	13.1%	24.5%	8.2%	14.2%
Angled (20–70°)	26.2	29.2	28.7	19.9
Vertical (70–90°)	45.9	1.0	41.4	2.5
Deformable	10.7	41.2	19.9	62.4
Mixed	4.2	4.2	1.7	1.1
Total	100.1	100.1	99.9	100.1
Diameter	(n=887)	(n=407)	(n=821)	(n=366)
<2 cm	4.1%	20.2%	10.7%	42.4%
2–5 cm	41.2	33.9	41.3	17.5
6–10 cm	38.0	25.1	32.3	16.7
11–15 cm	10.3	6.9	9.3	7.1
>15 cm	1.9	1.5	1.5	1.1
Mixed	4.7	12.6	5.0	15.3
Total	100.2	100.2	100.1	100.1

Inclination of Supports in Take-Off and Landing

Take-off.

Significant differences were observed between the species in the use of supports of various inclinations for leap take-off ($\chi^2=329.03$, $P<0.001$; Table VI). Horizontal supports were used approximately one-half as often by *Pithecia* compared to *Chiropotes*, while angled supports were used almost equally by both species. *Pithecia* most often used vertical or near-vertical supports for take-off, in contrast to the rarity of their use by *Chiropotes*. Deformable supports were used less by *Pithecia* than by *Chiropotes*. Supports of mixed inclination were used equally by both species.

Landing.

Landing support inclination also differed ($\chi^2=287.49$, $P<0.001$), with horizontal supports used less by *Pithecia* than by *Chiropotes*. Angled (particularly vertical) supports were used more frequently by *Pithecia* than by *Chiropotes*. Deformable supports were used by *Pitheci* much less frequently than by *Chiropotes*, for which these were the most common landing substrate used. Supports of mixed inclination were used infrequently by either species.

Diameter of Supports in Take-Off and Landing

Take-off.

Differences in take-off support diameter were notable ($\chi^2=126.24$, $P<0.001$; Table VI). *Pithecia* used the smallest branch size (<2 cm) only rarely, while *Chiropotes* did so in one-fifth of its samples. Both species used the second support size (2–5 cm) frequently, *Pithecia* more so than *Chiropotes*. Supports that were 6–10 cm in diameter, and those of the 11–15-cm size class were both used more by *Pithecia* than by *Chiropotes* for leap take-offs. Supports thicker than 15 cm were little used by either species, and supports with mixed diameters (usually smaller than 5 cm) were less often used for take-off by *Pithecia* than by *Chiropotes*.

Landing.

Landing support sizes also differed between the two species ($\chi^2=222.97$, $P<0.001$), with the smallest support class used less frequently by *Pithecia* than by *Chiropotes*. Supports of 2–5 cm were those most frequently used by *Pithecia* for landing; both this size class and the next larger one (6–10 cm) were used more by *Pithecia* than by *Chiropotes*. The larger support classes were used by both species approximately equally, although the largest were infrequently used by either species for landing. Again, mixed supports were used more by *Chiropotes* than by *Pithecia*.

Qualitative Aspects

The qualitative aspects of leaping in both species may be observed in Fig. 2, which was diagrammed from still video frames and demonstrates a ‘‘typical’’ representative leap for each species. To facilitate a comparison, this example shows both species beginning from a similar crouched take-off position; however, *Pithecia* more often takes off from a vertical cling. It should be kept in mind that leap characteristics depend on both landing and take-off substrates. The preparatory phase was similar between the species: the animals quickly lowered their body into a crouch by limb and back flexion, followed by immediate

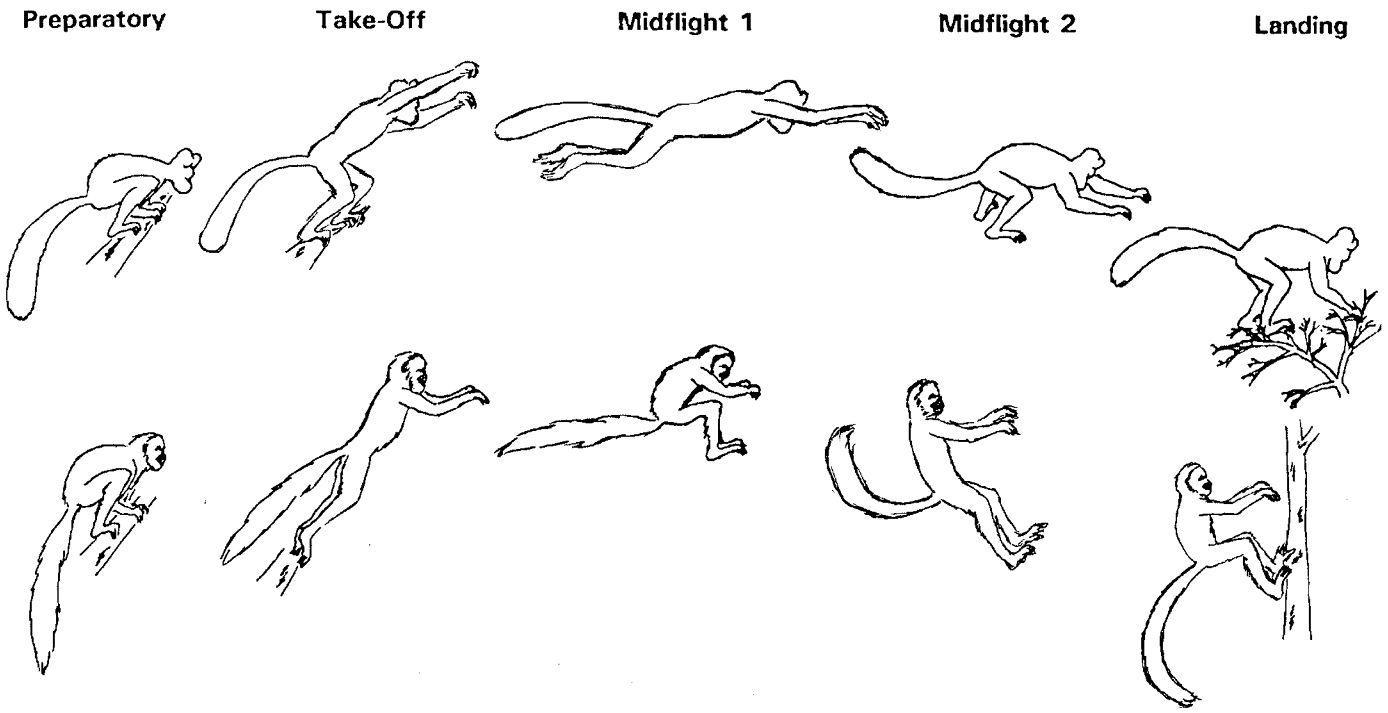

Fig. 2. Phases of leaps in *Pithecia* (bottom) and *Chiropotes* (top).

extension of the hindlimbs and back to initiate take-off. Subsequent leap phases differed between the species.

In *Pithecia*, extension of hindlimbs and back at take-off resulted in a highly angled body orientation that was maintained through the take-off phase. After the feet provided the propulsive thrust against the support, and take-off was complete, the fully extended hindlimbs began to be flexed at the hips and the knees. This flexion continued until the body was tucked into a ball, with back flexed and head down (Fig. 2, Midflight 1). The orthograde body orientation was most apparent at the leap's midpoint, when the body was tucked and the hindlimbs were flexed approximately 90° at the hips and the knees. *Pithecia* subsequently began to extend the hindlimbs, immediately followed by back extension (Fig. 2, Midflight 2). The tail was raised, the upper body became angled slightly posteriorly, and hindlimb extension continued as *Pithecia* approached the landing target. The almost fully extended hindlimbs contacted the support first, causing flexion first at the hips and knees, and then the back and forelimbs, as the latter contacted the landing substrate; the tail was lowered (Fig. 2, Landing). The hindlimbs continued to flex until the body was at rest on the landing substrate. *Pithecia* leaps were usually 2–4 m, but could reach at least 5 m in a straight or slightly parabolic plane, with little downward displacement.

From its crouching position, *Chiropotes* quickly extended its back, lifting the upper torso and moving it forward. After it pushed off against the support, the forelimbs began to be protracted and abducted, which continued until the elbows were approximately lateral to the head, and the forelimbs were in nearly full extension. Back extension continued, and the hindlimbs were extended distally to the plantar flexion of the feet for take-off propulsion. At this point, the torso was angled only slightly upward (Fig. 2, Take-Off). Immediately after take-off, the hindlimbs and the back were almost completely extended, and the forelimbs fully protracted, with the body in a pronograde orientation (Fig. 2, Midflight 1). After maximum hindlimb extension was reached, *Chiropotes* began to flex hindlimbs at the hip and knee, and abduct at the hips; the forelimbs were also abducted (Fig. 2, Midflight 2). Flexion continued, with the back also flexing as the body drew closer to the landing substrate. Since a pronograde trunk orientation was usually maintained throughout the leap, all four limbs were at approximately the same level at landing (Fig. 2, Landing), if the landing substrate was the typical horizontal support or deformable multiple branches. Upon impact, the limbs underwent flexion as compressive landing forces were transmitted through the body. *Chiropotes*' leaps were typically less than 2 m, and were greater only when a downward component was involved, in which case the covered distance could be several meters, and landing was virtually always onto flexible terminal branches.

DISCUSSION

The observable differences between *P. pithecia* and *C. satanas* in their leaping behavior and associated habitat use by are supported by statistical significance, and are in agreement with previous work on Suriname pitheciins [Fleagle & Mittermeier, 1980]. Fleagle and Mittermeier [1980] also found that leaping was far more prevalent in *Pithecia* than in *Chiropotes*. While the leaping rates for *Chiropotes* are comparable between the two studies (18% compared to 25% for this study), a much higher leaping frequency (75%) was reported for *Pithecia* in Suriname (also see below). A summary of the primary differences between the two species is presented in Table VII.

TABLE VII. Summary of Observed Differences Between *Pithecia pithecia* and *Chiropotes satanas*

	Pithecia pithecia	*Chiropotes satanas*
Body mass	Smaller (~1.6 kg)	Larger (~2.8 kg)
Frequency of leaping during travel	40%	25%
Most frequent take-off position	Postural; Vertical cling	Locomotor: pronograde clamber
Landing	Hindlimb-first	All four limbs
Canopy height while leaping	Lower	Higher
Primary tree portions used for take-off	Lower tree portions	Crown and terminal branches
Primary tree portions used for landing	Lower tree portions	Terminal branches
Most frequent take-off substrate	Vertical supports	Angled or horizontal supports
Most frequent landing substrate	Single, vertical support	Multiple, deformable supports
Body orientation during leap	More orthograde	More pronograde
Leap length	Longer	Shorter

Influence of Habitat Structure and Habitat Use

Habitat structure.

Support availability and choice are said to be important influences on positional behavior [e.g., Cant & Temerin, 1984; Crompton et al., 1993; Garber, 1984; Mendel, 1976; Ripley, 1979; Warren, 1997]. Extensive analyses of both species' habitats were undertaken to gauge canopy connectedness and the availability of various support inclinations in relation to the primates' choice of support [Walker, 1996]. An important difference was the higher frequency of emergent trees on the "*Chiropotes*" island compared to the "*Pithecia*" islands, which resulted in a less continuous canopy for the former. *Chiropotes* commonly feeds in these emergent trees, and consequently performs more dropping or downward leaping when it changes forest levels [Walker, 1996]. Although there is greater homogeneity in tree size on the "*Pithecia*" islands, *Pithecia* often descend to leap between the lower tree portions. This is consistent with previous studies that reported more leaping in lower forest levels [Crompton, 1984; Davies, 1984; Kinzey, 1976; Fleagle, 1978; Fleagle & Mittermeier, 1980].

While some differences in support availability correspond accordingly with differences in support use (e.g., *Pithecia's* less frequent use of horizontal supports, and greater use of angled supports and lianas corresponds to the availability of such in their habitats), others differed from expectation [Walker, 1996]. Primarily, the similar proportions of vertical branches in both species' habitats indicate that their more frequent use by *Pithecia* is largely independent of availability and is driven by preference. Likewise, support preference rather than availability appeared to characterize positional behavior differences between *Lepilemur edwardsi* and *Avahi occidentalis* at Ampijoroa, Madagascar [Warren, 1994].

Habitat use.

Take-off and landing supports largely determine leaping characteristics [Dunbar, 1988; Crompton et al., 1993], and the use of tree portions and substrates is closely intertwined with take-off position, leap distance, and body orientation. The solid vertical supports common to lower tree portions are those typically selected by *Pithecia* for leap take-offs and landings, particularly for longer leaps [see also Warren & Crompton, 1997]. Solid supports require less force to be generated at take-off compared to compliant ones, which lose energy to the substrate [Alexander, 1991; Demes et al., 1995]. This allows for greater leap distance and thus more time to attain the vertical body orientation necessary for a hindlimb-first landing.

Many (41%) of *Chiropotes*' leap take-offs are initiated from deformable supports, which limits the amount of propulsion to be generated. C*hiropotes*' leaps are thus much shorter than those of *Pithecia*, with the exception of downward leaps. *Chiropotes*' most frequent landing target is the flexible terminal branches, particularly after a long leap. This is common in quadrupedal primates [Crompton et al., 1993; Garber, 1980; Mittermeier & Fleagle, 1976; Morbeck, 1976; Ripley, 1967; Schön Ybarra, 1984; Warren & Crompton, 1997].

Warren and Crompton [1997] found that specific differences in habitat use between *Avahi* and *Lepilemur* appeared to contribute to niche separation. The same may be true for *Pithecia* and *Chiropotes*, two specialized seed predators that are sympatric throughout much of their range. Preferred routes through the habitat are chosen to best combine the minimization of energy costs and locomotor risks with predator avoidance [Warren, 1994].

Influence of Body Size and Morphology on Leaping

Body size influences how an animal negotiates its habitat, and the behaviors that are the most efficient for a given environment select for an ‘‘optimal’’ morphological configuration, with allometric effects placing limits on form [Jouffroy & Lessertisseur, 1979; Jungers, 1984]. Animals of various sizes experience the same habitat in different ways (e.g., a gap in the forest is relatively larger for a smaller animal [Cartmill & Milton, 1977; Fleagle & Mittermeier, 1980]), and branch compliance differs for animals of various body sizes [Demes et al., 1995]. Cartmill and Milton's [1977] prediction that body size would be negatively correlated with leaping was corroborated by Fleagle and Mittermeier [1980] in a study of several sympatric Suriname primates. Likewise, the smallest pitheciin species, *P. pithecia*, appears to leap more than either its conspecifics (*P. monachus* and *P. albicans*) or closely related genera (*Chiropotes* and *Cacajao*) [Fleagle & Mittermeier, 1980; Happel, 1982; Peres, 1993; Walker, 1996]. However, Gebo and Chapman [1995] found that leaping increased with body size in five sympatric Ugandan cercopithecids. These results dictate that one should use caution in making generalizations involving distantly related taxa, each of which has a unique phylogenetic history. It may be more instructive to examine lower taxonomic levels for such associations, where the confounding variable of evolutionary history may be controlled.

While leaping is considered a single behavioral category, the qualitative differences between species may select for different morphological features [Terranova, 1996]. Thus, it is important to consider not only the frequency of a given behavior, but also the manner in which it is carried out. A single set of ‘‘leaping adaptations’’ does not exist, but various morphologies are associated with different behavioral variations of leaping, influenced by body size [Anemone, 1990; Demes & Günther, 1989; Demes et al., 1995; Oxnard et al., 1981]. For example, smaller leapers (e.g., *Galago moholi* and *Tarsius*) have evolved morphological specializations that increase the relative hindlimb length to generate greater take-off forces, while larger leapers (e.g., *Galago crassicaudatus*, *Avahi*, and *Propithecus*) can generate sufficient force because of their absolutely longer hindlimbs, and are thus less specialized in their morphology [Crompton et al., 1993; Demes & Günther, 1989; Emerson, 1985].

Pithecia exhibits numerous morphological features that provide a biomechanical advantage for leaping and clinging, many of which parallel adaptations made by vertical clinging and leaping prosimians [Fleagle & Meldrum, 1988] (Table VIII). The skeletal features of the larger *Pithecia* species, which leap less often than *P. pithecia*, exhibit limb proportions and a femoral morphology that resemble *Chiropotes* more than *Pithecia pithecia* (Meldrum, personal communication, personal observation). Napier and Napier's [1967] assessment that the intermembral index is highly similar between *Pithecia* and *Chiropotes* (contra Fleagle and Meldrum [1988]) probably reflects the fact that they reported on one or more of the larger *Pithecia* species, and not on *P. pithecia*.

Biomechanical Considerations

Maximizing leap distance.

Both *Pithecia* and *Chiropotes* exhibit behaviors that appear to maximize leap distance, relating primarily to generating sufficient acceleration at take-off. These behaviors include 1) the use of a pre-leap crouch at take-off, 2) the use of the limbs in a "temporal sequence pattern," and 3) the choice of appropriate take-off and landing supports.

The take-off position often incorporates a briefly assumed crouching posture by rapid limb and back flexion, followed by immediate extension of these body segments at take-off. Such forcible stretching of muscle fibers and/or tendons while under tension (i.e., during eccentric muscle contraction) results in absorption of mechanical energy [e.g., Cavagna, 1977], which can be stored in muscle fibers or tendons for reutilization in subsequent active contraction [Emerson, 1985]. This "potentiation" enhances power output, and has been demonstrated for kangaroos [Alexander & Vernon, 1975] and discussed for large prosimian vertical clinger and leapers [Demes et al., 1995]. In *Pithecia*'s continuous leaps, muscles that are stretched at one leap's landing may provide some energy for subsequent take-off. However, energy storage and its subsequent utilization are dependent on tendon length and compliance, muscle fascicle length, and branch compliance [Alexander, 1991].

To increase the amount of time over which muscular force is applied to the take-off support, the limbs and the back may be used in a "temporal sequence pattern" (R. Robertson, personal communication). The process begins with extension of the back and forelimbs, followed by hindlimb extension from the proximal to the distal limb segments. The final propulsive thrust comes from the action of the calf muscles, which provides plantar flexion against the support.

Support choice is discussed above in terms of the affect of rigidity vs. compliance on leap distance.

Control of leap direction and preparation for landing.

In leaping from one vertical support to another, a primate must rotate the body 180° to prepare for landing [e.g., Dunbar, 1994]. Rotation about the body's longitudinal axis is initiated at take-off, and is halted by a lateral swing of the tail as the body turns in mid-air to face the landing support [Dunbar, 1988; Peters & Preuschoft, 1984]. This lateral tail swing is noted in *Pithecia* but not in *Chiropotes*, which does not exhibit body rotation during leaping. The ball shape

TABLE VIII. Selected Morphological Correlates of Leaping and Clinging Behaviors Exhibited by *Pithecia pithecia* [Fleagle & Meldrum, 1988]

Features relating to:	Morphology
Adducted hindlimb excursion, limited rotation/lateral movements:	● Articular surface of femoral head extends more postero-superiorly, fovea capitis distally located, femoral neck set approximately perpendicular to shaft
	● Femoral condyles more symmetrical from posterior aspect, pronounced adductor tubercle
	● Proximal tibial shaft medio-laterally compressed
	● Distal 10–20% of tibia and fibula often joined by connective tissue, sometimes fused
	● Fibula and tibia slender, medio-laterally compressed
Increasing distance and time over which muscular force can be applied, and absorption of compressive forces at landing:	● Increased length of hindlimb; mean intermembral index of *Pithecia* is 76, compared to 83 in *Chiropotes*
	● Increased length of digit rays of foot and cuboid
	● Higher number of lumbar vertebrae relative to thoracic in *Pithecia* than in *Chiropotes* (back extension)
Resist bending forces while leaping:	● *Pithecia's* short femoral neck
Muscular advantage:	● Unique aspect of vastus lateralis muscle; distinctive in *Pithecia* for extensive development and proximal origin
	● Greater trochanter (origin of vastus lateralis) broad, proximally flattened, overhangs femoral shaft anteriorly
Prevention of patellar displacement during leaping:	● Lateral side of patellar groove somewhat expanded
Capability for extreme dorsiflexion (in clinging):	● "Tibial stop": extension of anterior surface of talar trochlea onto dorsal surface of talar neck
Capability for powerful humeral retraction in *Pithecia*, habitually flexed elbow (correlates with frequent clinging):	● High brachial index (92) in *Pithecia* (compared to 86 in *Chiropotes*)
	● Large flange on scapula (for origin of teres major muscle), which can lengthen muscle's moment arm
	● Almost cylindrical (rather than lipped) humeral trochlear shape
	● Extension of proximal portion of anterior trochlear surface onto humeral shaft

("tuck") assumed by some vertical clingers and leapers, including *Pithecia*, serves to minimize the mass moments of inertia about the animal's transverse axis, because the body is most easily rotated while tucked [Peters & Preuschoft, 1984]. Thus, the lower body is rotated forward as the hindlimbs and back are extended, so the feet can contact the landing substrate first [see also Dunbar, 1988; Niemitz, 1983; Peters & Preuschoft, 1984; Terranova, 1996]. Since such specialized maneuvers are required for hindlimb landing [Dunbar, 1988; Peters & Preuschoft, 1984], the mechanical advantage of absorbing landing forces in this way must be significant.

Why Leap?

Saltation has long been associated with escape behavior in animals, since it provides both quick locomotion and the ability to briefly startle a potential attacker [Walton & Anderson, 1988]. For example, its evolution in frogs may have allowed for their rapid return to the water when threatened by terrestrial predators [Gans & Parsons, 1966]. In various primates, leaping has been associated with escape behavior even for species that are categorized as arboreal quadrupeds [Cant, 1988; Crompton, 1984; Fleagle et al., 1981; Gebo et al., 1994]. Fleagle and Mittermeier's [1980] report of high leaping rates (75%) for *P. pithecia* in Suriname may have resulted from its unhabituated status, and in another study the leaping rates of *Colobus badius* increased when they were presented with experimentally produced threatening situations (i.e., playbacks of predator vocalizations, and approach of observers) [Gebo et al., 1994]. Additionally, in *Pithecia* and in specialized vertical clinging and leaping prosimians, the frequent use of solid supports for take-off and landing ensures quieter movement through the forest and can thus enhance predator avoidance.

Awareness of the context in which positional behaviors occur can help us determine their biorole, and thus to make inferences about their evolutionary significance. As mentioned above, Warren and Crompton's [1977] study indicates that differences in support choice and associated positional behaviors may contribute to niche separation in *Lepilemur* and *Avahi*. In the case of *Pithecia* and *Chiropotes*, the historical threat of competition with early *Chiropotes* may have driven the smaller *Pithecia* to lower forest levels [Peres, 1993; Walker, 1996], where it may have experienced increased vulnerability to predators. In a microhabitat where vertical supports predominate, leaping would provide the most effective means of escape.

Implications of Differences Within a Positional Behavior Category

These results have implications for the use of locomotor classifications, interpretation of fossils, and elucidating the evolutionary significance of positional behaviors. While locomotor classifications are heuristically important, each behavioral category should be examined in terms of the qualitative differences between species, and the influence of scaling effects. Differences in morphological features may reflect the various manners in which the "same" behavior is exhibited, as demonstrated by the differences in the leaping behaviors of *Pithecia* and *Chiropotes*. Demes and Günther [1989] also pointed out the limitations of classic methods of classifying locomotor behavior. Solutions may include the construction of more fine-grained locomotor classifications, and devising categories with anatomically meaningful definitions [e.g., Hunt et al., 1996; Jolly, 1965].

CONCLUSIONS

The differences noted between the leaping behaviors of *Pithecia* and *Chiropotes* do not diverge from one another in a direction predicted by differences in their habitats. Rather, preferences for particular tree portions and the supports within seem to provide the major influence. *Pithecia* uses mainly solid vertical supports in lower tree portions for leaping substrates, while *Chiropotes* uses low-angled deformable supports of the main crown and terminal branches. The characteristics of these substrates influence take-off and landing position, as well as leap distance.

Pithecia's smaller body size may have required morphological adaptations to deal with the energetic demands of leaping; these features parallel those of other specialized vertical clingers and leapers, and are unique among anthropoids. Behavioral parallels are also apparent and include the frequent use of solid supports for take-off, take-off from a postural rather than a locomotor position, vertical body orientation and tucking during leaps, and hindlimb-first landings onto solid supports. *Chiropotes* demonstrates components of leaping behavior indicative of its generalist position [Hildebrand, 1982], including the use of momentum from locomotor behaviors to initiate leaps, pronograde body orientation in mid-flight, and frequent use of flexible landing substrates to absorb compressive forces. *Chiropotes* lacks morphological features associated with leaping.

The finding of such variation within a behavioral category can contribute to our understanding of form/function relationships, and thus to the accuracy with which we reconstruct the positional behavior of extinct species.

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