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Body size and leaping kinematics in Malagasy vertical clingers and leapers

The locomotor category of vertical clingers and leapers has been dominated conceptually from the beginning by its small-bodied representatives, galagos and tarsiers. Over the years, great morphological diversity has been documented within the group, much of it size-related. Corresponding behavioral differences remain to be explored, in large part because adequate data on the larger-bodied species were not available. The primary objective of this paper was to characterize the leaping kinematics of indriid primates, the much neglected large-bodied vertical clingers and leapers. We videotaped leaps of four species of indriids at four different sites in Madagascar: *Indri indri*, *Propithecus diadema*, *Propithecus verreauxi*, and *Avahi laniger*. Video images were evaluated qualitatively and quantitatively after importing them into a computerized measuring program. Ranges of motion at the hip joint (a combination of extension, adduction, and medial rotation) probably exceed those of tarsiers and galagos. The foot of indriids usually releases the grip around the support and contributes little or nothing to propulsion, thus supporting the notion that indriids are "hip" leapers. With the forefoot stationary on the support, hindfoot eversion accommodates the adduction and medial rotation at the hip during acceleration for take off. Indriid leapers can be characterized as "tarsirotators" in contrast to "tarsifulcrumating" galagos and tarsiers. Size-related variation in hindlimb kinematics is surprisingly limited within the sample of indriid leapers, although acceleration time (the duration of the push off) does increase with increasing body size. In addition, forelimb kinematics reveal a clear size-related pattern; the smallest indriid species leaps with its arms tucked into the chest—like tarsiers and galagos—and the larger-bodied indriid species use their arms during acceleration for take off as well as to initiate body rotation while airborne. The small-bodied species rely exclusively on their tails for this same purpose. Whereas relative tail length decreases with increasing body size in vertical clingers and leapers, the relative weight of the forelimbs increases and makes their action more effective.

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Introduction

Vertical clinging and leaping (VCL) is one of the most striking locomotor behaviors among primates. Vertical clingers and leapers as a group are united by unique postural and locomotor habits: they cling on to and leap from and to vertical supports. Despite the apparent uniformity of the behavior in these mostly prosimian primates, and the initial efforts by Napier & Walker (1967) to identify a suite of morphological features characterizing the group, most subsequent studies have emphasized the morphological diversity within vertical clingers and leapers, associated with both phylogeny and size (Cartmill, 1972; Martin, 1972; Szalay, 1972; Stern & Oxnard, 1973; Jouffroy & Lessertisseur, 1979; Oxnard *et al.*, 1981; Gebo & Dagosto, 1988; Godfrey, 1988; Covert, 1988; Demes & Günther, 1989; Anemone, 1990; but see Fleagle & Anapol, 1992). To this point, no attempt has been made to explore whether the morphological variation seen in VCL species is matched by a similar variation in locomotor kinematics and performance. Research on leaping kinematics has focused almost exclusively on galagos and tarsiers, the small-bodied VCL species. Similarly, almost all biomechanical models have targeted leaping at small body size, and functional hypotheses regarding leaping adaptations

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are, therefore, heavily biased towards small-bodied leapers (Hall-Craggs, 1965; Treff, 1970; Jouffroy & Gasc, 1974; Niemitz, 1984*a*; Peters & Preuschoft, 1984; Günther, 1989; Günther *et al.*, 1991; Crompton *et al.*, 1993).

Clearly, a major obstacle in our understanding of musculoskeletal diversity within the vertical clingers and leapers is the lack of adequate locomotor data on a range of large-bodied indriid leapers. As both a distinct phylogenetic group and the largest of the vertical clingers and leapers, indriids can provide a broader mechanical and evolutionary perspective on this unusual aspect of primate locomotion. For a clear understanding of the functional and phylogenetic factors that have led to the morphological diversity among vertical clingers and leapers, it is critical that we examine both the differences between indriids and other prosimian leapers as well as any size-related trends evident within indriids.

Our analysis is based on video films of four species of indriids in their natural habitats in Madagascar. These videos were analyzed to develop a locomotor profile of indriid leaping. The focus of this paper is on the kinematics of take offs. Higher take off than landing forces characterize the larger-bodied vertical clingers and leapers, and the take off (rather than the landing) may, therefore, be critical in interpreting leaping behavior and related features of body design in these animals (Demes *et al.*, 1995, 1996).

Animals and sites

Videos were taken at four sites in Madagascar of animals habituated earlier in the context of other projects. A Canon L1 Hi8 camera with a ×15 zoom lens was used on a tripod or unipod. From a total of 24 h of videotapes collected over a period of 2 months, leaps were edited on to one tape and subsequently analyzed frame by frame. Table 1 lists the number of locomotor events available for analysis, specified by species, substrate size and orientation. Specific observations and quantitative analyses are based on subsets of the total number of take offs that were selected to be appropriate for the question under consideration; e.g., close-ups for foot positions, lateral views for angles of flexion, or posterior views for abduction angles (see below). Samples for all species cover a range of leaping distances which were not quantified.

Propithecus verreauxi was filmed at two sites, Ampijoroa (*P. verreauxi coquereli*) and Berenty (*P. verreauxi verreauxi*). In the dry, deciduous forest at Ampijoroa, the animals travel most of the time high up in the crowns of trees, leaping from and into the canopy. The comparatively high number of oblique and horizontal take off supports for this species reflects this habitat preference (Table 1). The landings are often in a "monkey-like" fashion, with the limbs spread out and grabbing several branches for support. We observed one animal falling out of a tree, and, according to our local guide, this was not a singular event.

At Berenty, *P. verreauxi* was filmed in the spiny forest where the animals moved on Didiereaceae, as well as several other species of trees, most of which also had thorns. The long distance jumps were usually low on the Didiereaceae, where the spines are not as long and dense as higher up. However, the animals were also frequently observed in the upper parts of these plants, where the spines are long and so densely packed that it is impossible to contact the substrate in between them. Occasional hand and foot adjustments were seen when the animals were climbing or clinging, with a hand or a foot pulled back from the initial grasp and repositioned. In close-ups, hands and feet were regularly seen in contact with spines—something that we found quite painful when we tried it ourselves.

Table 1 Sample for kinematic analysis

Species	Body mass* (kg)	Leaps (n)	Take off support						Sites
			Orientation†			Size‡			
			Verticle	Oblique	Horizontal	Small	Medium	Large	
Avahi laniger	1·10	8	5	1	2	2	5	1	Ampijoroa, Perinet, Ranomafana
Propithecus verreauxi	3·55	119	73	27	19	41	41	37	Ampijoroa, Berenty
Propithecus diadema	5·70	66	43	19	4	26	36	4	Ranomafana
Indri indri	6·50	57	45	8	4	17	32	8	Perinet

*Mittermeier *et al.*, 1994; values are means for two subspecies of *A. laniger* and two subspecies of *P. verreauxi* represented in our sample; the *P. diadema* weight is for the subspecies *P.d. edwardsi*.

†Orientation was catalogued in three categories: vertical ± 20°, horizontal ± 20°, and oblique=everything in between.

‡Support size was assessed relative to the size of the animals' feet: small=one foot can grip around; medium=two feet can grip around; large=everything greater than the span of two feet.

Two groups of *Propithecus diadema edwardsi* were filmed in the rain forest of Ranomafana National Park. In the study area secondary forest predominates, and animals travel on small- to medium-sized tree trunks (*cf.* Dagosto, 1995).

All footage of *Indri indri* is from one habituated group of animals in the secondary forest of Andasibe (Perinet). Whereas the animals sleep and feed in the canopy of the relatively few tall trees, they travel between the trunks of the more numerous smaller trees, lower in the vegetation.

The few *Avahi laniger* leaps were recorded at Ampijoroa (*A. laniger occidentalis*), Andasibe, and Ranomafana (*A. laniger laniger*). The animals were filmed when leaving their sleeping trees late in the afternoon. We were unable to follow them beyond the initial leaps.

Kinematic methods

Quantification of kinematic parameters from films recorded in the wild can be problematic. The camera is often positioned at an angle to the animals' plane of movement, which leads to distortions in distances and angles. Joint angles were therefore measured only on selected sequences with the camera roughly at the same height as the animal and not laterally tilted against the plane of angular movement. Acceptable camera height was frequently achieved in the hilly terrains of Andasibe and Ranomafana and also occurred regularly at Ampijoroa and Berenty when the animals traveled at low heights. Appropriate video images were A/D converted and imported into a Macintosh computer. MacMorph morphometrics software (Spencer, 1995; Spencer & Spencer, 1995) was used for measuring angles from the digital images. Without marker points on joints and other fixed landmarks on the animals' bodies (as in standard laboratory kinematic analyses), the measuring error was higher than desirable. The angular measurements could be reproduced within 10° and should be regarded as good approximations. Additional variables were sorted into gross categories and yet others described qualitatively. A more detailed description of data collection methods is provided below.

Take off angles are the angles of the animal's trajectory from the take off support. The take off trajectory connects the approximate center of gravity of the animal at the moment of toe off with the substrate contact point. The position of the center of gravity varies with body posture. We estimated the center of gravity for cardboard animal outlines drawn from videoimages selected at the moment of toe off. For all four species it is within the lower pelvic region (in posterior view slightly above the base of the tail). This position was subsequently chosen as an approximation for the actual center of gravity. To assess the error introduced by this rather crude method we moved the position of the center of gravity around in the lower abdominal region. Variation of the measured angle was under 5°, which is well below the variation in take off angles for different leaps (see below).

For the hip, the amount of crouching that precedes acceleration for take off was quantified in a subset of sideviews. The knee was used as a "pointer" relative to the trunk, its position being counted as "in the midaxillary line", or "dorsal" or "ventral" to it. Abduction of the hip was measured as the angle between the long axis of the thigh and the midline of the trunk in selected posterior views of take offs, again with the camera positioned at approximately the same height as the animal. External rotation was estimated from the amount the knees were projecting outward halfway through acceleration for take off, when the knees were most clearly visible.

In order to evaluate the contribution of the foot in accelerating the body before take off, the contact of the foot with the substrate was categorized, in selected video close-ups, as being

Table 2 Preparatory movements

Species	Countermovement		Type of movement*			Foot adjustment†	
	n	Occurence	n	Crouch	Hop	n	Occurence
Avahi laniger	7	6 (86%)	6	5 (83%)	1 (17%)	7	3 (43%)
Propithecus verreauxi	64	61 (95%)	61	44 (72%)	17 (28%)	64	36 (56%)
Propithecus diadema	47	46 (98%)	46	27 (59%)	19 (41%)	47	31 (66%)
Indri indri	33	31 (94%)	31	10 (32%)	21 (68%)	33	26 (79%)
Test for interspecific differences‡		$P>0.05$		$P<0.05$			$P>0.05$

*Animals either go into a deep crouch or perform a small, preparatory hop.
†Foot adjustments can occur with both types of countermovements.
‡Row by column test of independence (Sokal & Rohlf, 1981).

located in the forefoot, the midfoot or the hindfoot, and the orientation of the toes relative to the substrate long axis and the take off trajectory was registered. Angular excursions in the sagittal plane were estimated on selected lateral views as angles between the leg and the forefoot; i.e., these angles comprise ankle, midtarsal, and tarsometatarsal joint movements. The amount of inversion and eversion was assessed from the orientation of the plantar surface of the hindfoot at the beginning and the end of acceleration for take off.

Acceleration times were recorded by counting the videoframes from the beginning of hindlimb extension to toe off. One videoimage corresponds to 1/30 of a second. For *A. laniger*, sample frequency was doubled by splitting videoimages into their two consecutive fields.

Results

General kinematics
Preparatory countermovements. Take offs are routinely preceded by a preparatory movement opposite to the direction of the take off vector ("initial countermovement", Table 2). The animals go into a deep crouch and lower their trunks between the abducted thighs. Frequently, an initial hop into this crouched position was observed (Table 2). Such forceful countermovements (bounces) were performed more often by the larger-bodied species. The animals often reposition themselves on the substrate, adjust their body position relative to the target substrate and reposition their feet for take off.

Head and body rotations. Target substrates of vertical clingers and leapers are usually behind the animal as it clings to the take off substrate. When aiming at the target substrate, head and neck rotations of 180° are not unusual, with the animal looking backwards over its shoulder (Figure 1). The fact that the target is behind the animal also requires a rotation of the animal about its long axis in order to land front first. This rotation is initiated during acceleration for take off and performed when the body is fully extended (Figure 1). In this position, the moment of inertia of the body about the long axis is minimal, and subsequently, the necessary torque is small. The spin is probably generated by an asymmetrical push off (i.e., with different amounts of force at the two feet) and in the larger-bodied species assisted by forceful movements of one forelimb that is released from the substrate and swung upward and outward (see also below). In most leaps rotation about the long axis is completed shortly after toe off.
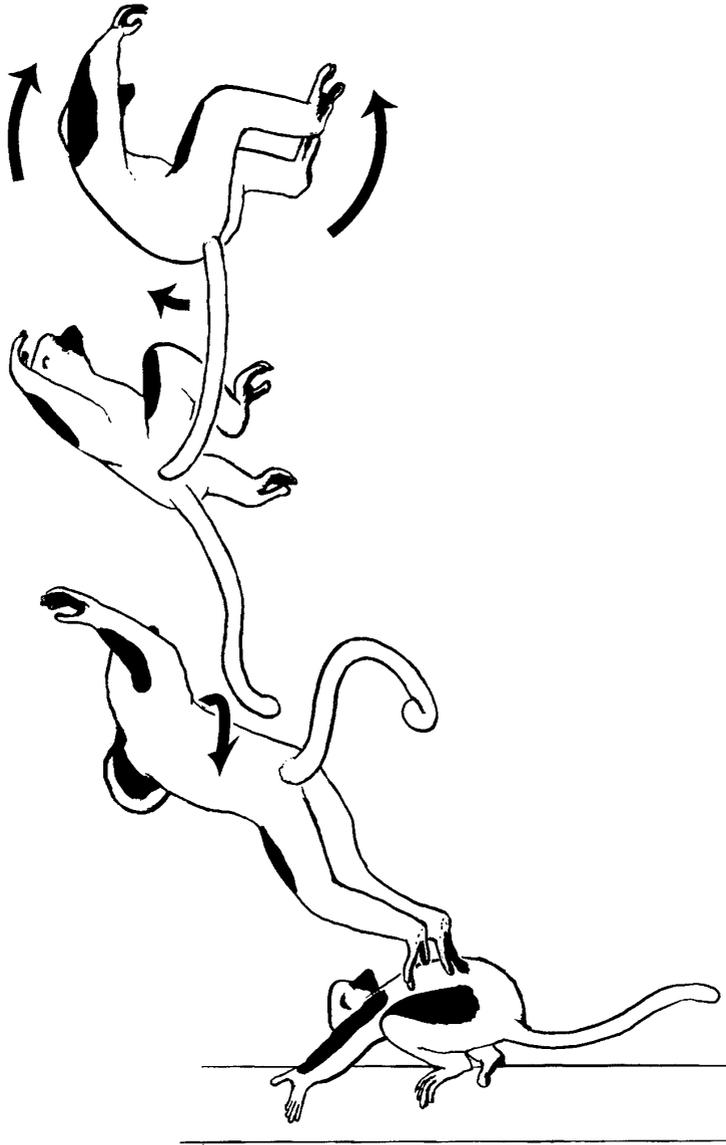
Figure 1. A leap of *Propithecus verreauxi*, drawn from consecutive videoimages. Note the extended body posture during rotation about the longitudinal axis and the crouched posture during rotation about the transverse axis, as well as arm and tail movements.

Table 3   **Take off trajectory angles**

Species	n	Angle (degrees) Mean ± 1 S.D.	Range
Avahi laniger	3	45 ± 10	35–55
Propithecus verreauxi	12	50 ± 19	40–70
Propithecus diadema	5	43 ± 6	35–50
Indri indri	10	45 ± 8	30–55

Angles were measured between the foot contact on the take off substrate and the approximated center of gravity at toe off. The mean values are not significantly different from the optimum of 45°.

Indriids invariably land with their hindlimbs first. They, therefore, also have to perform a rotation about a transverse axis to bring the hindlimbs into landing position. This rotation is executed while the animals are airborne; i.e., with no forces (other than air resistance) acting on the animal's body. Before rotation about the transverse axis is initiated, the animals flex and abduct their long and heavy hindlimbs so that they can be brought up to the side of the trunk (Figure 1), thus reducing the moment of inertia of the lower body. Because of the conservation of momentum, subsequent rotation of the hindlimbs into a position in front of the trunk has to be accompanied by movements of other parts of the body that have an opposite rotating effect of equal magnitude on the center of gravity. Large-bodied indriid leapers (*Propithecus, I. indri*) swing their extended forelimbs downward, like long jumpers before landing (Hochmuth, 1984). The arms are extended to increase the moment of inertia of the upper body. The tail, when present, assists this movement and is swung upward causing the lower body to swing forward (Peters & Preuschoft, 1984; see also below). *A. laniger* video footage is limited to take offs, and does not enable us to evaluate midflight kinematics for this species.

Take off angles. Take off angles are highly variable with a range from 30–70°, and do not appear to differ between species (Table 3). The ranges for all species include the 45° angle that maximizes leaping distance (see any standard textbook of physics; Crompton *et al.*, 1993).

Acceleration times. On average, *A. laniger* accelerates over 119 ms, *P. verreauxi* over 172 ms, *P. diadema* over 205 ms, and *I. indri* over 210 ms. Robust analysis of variance indicates that there are significant differences in this regard among the species ($P < 0.001$). Post hoc pairwise comparisons (Tukey's LSD) disclose that all contrasts are significant except for the difference between *I. indri* and *P. diadema*. Acceleration times are highly and positively correlated with body size (Figure 2).

Hindlimb kinematics

Hip. All species initiate acceleration for take off with an extremely "bow-legged" body posture. During the deep crouch that is assumed prior to acceleration for take off, the trunk is lowered between the abducted and laterally rotated thighs. In the majority of quantified cases for *A. laniger* and *P. verreauxi*, the knees are beyond (i.e., dorsal to) the midaxillary line of the body (Table 4). In *P. verreauxi*, the knees are beyond the dorsal contour line of the animal's trunk for many take offs ($n = 10$ in the quantitative subsample, Figure 3). In 50% of the cases, *P. diadema* and *I. indri* begin acceleration for take off with more moderate flexion at the hip. In these
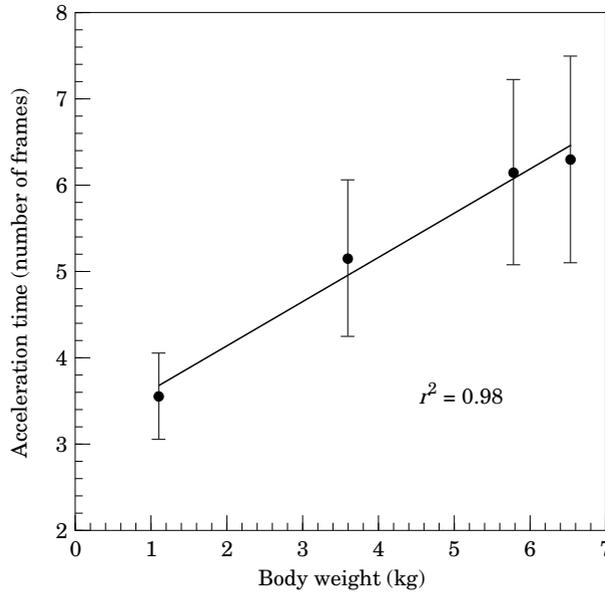
Figure 2. Acceleration times plotted against body mass. Dots represent the species means, and bars ± 1 S.D.; the line represents a best fit through the means. Acceleration times are given in number of frames with each frame representing 1/30 of a second. See Table 1 for information on body mass.

Table 4   **Hip flexion as indicated by knee position**

Species	n	Knee position*		
		Ventral	Midaxillary	Dorsal
Avahi laniger	3	0	1 (33%)	2 (67%)
Propithecus verreauxi	28	3 (11%)	5 (18%)	20 (71%)
Propithecus diadema	15	4 (27%)	3 (20%)	8 (53%)
Indri indri	10	2 (20%)	3 (30%)	5 (50%)
Test for interspecific differences†			$P>0.05$	

  *Knee position prior to acceleration for take off is scored relative to the midaxillary line.
   †Row by column test for independence (Sokal & Rohlf, 1981).

largest species, the knees were never observed posterior to the dorsal contour line of the body.

Measured angles of abduction at the beginning of acceleration for take off are between 41° and 63° (Table 5), with the larger-bodied species exhibiting more abduction than the smaller-bodied species [Figure 4(a)]. This difference is significant only in pairs *I. indri/P. verreauxi*, and *I indri/A. laniger* (Tukey's HSD; $P<0.01$ in robust analysis of variance). The thighs are still highly abducted and externally rotated midway through acceleration for take off [Figure 4(b)], with measured abduction angles of 40°–55° (Table 5), and with an estimated external rotation of 45° to almost 90°. The knees are pointing virtually laterally in many take offs. It is only in the second half of acceleration for take off that the thighs are medially rotated and adducted to almost neutral position at take off. Typically, the hip is fully extended at take
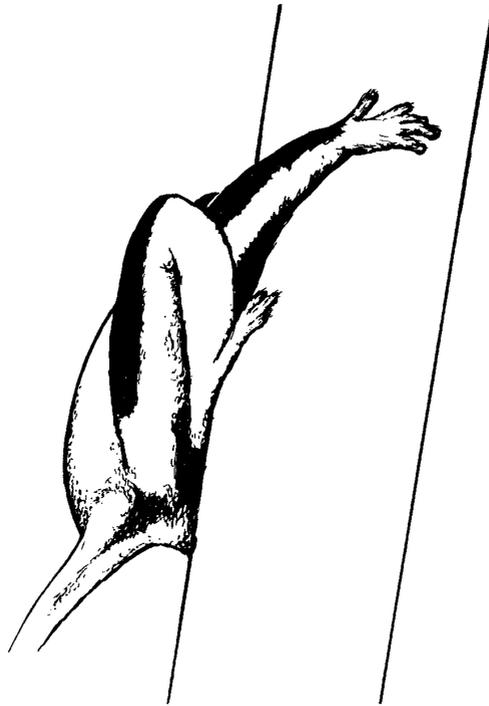
Figure 3. Deep crouching posture assumed before acceleration for take off. In *Propithecus verreauxi* the trunk is lowered between the abducted thighs often to such a degree that the knees project beyond the dorsal contour line of the body. Drawn from a videoimage.

Table 5   **Angles of abduction at the hip**

Species	Angle (degrees)	
	Before	Midway
Avahi laniger	42 ± 3 (3)	40 (1)
Propithecus verreauxi	41 ± 13 (4)	52 ± 5 (4)
Propithecus diadema	53 ± 10 (6)	40 ± 8 (6)
Indri indri	63 ± 6 (3)	55 ± 6 (3)

Values indicate the mean ± 1 S.D., and number of cases in parentheses of angles measured before and during acceleration for take off.

off (Fleagle & Anapol, 1992), except for short hops. Qualitative observations on the total sample of take offs are consistent with the smaller number of quantified cases.

Acceleration for take off at the hip joint is clearly a combined movement of extension, medial rotation, and adduction. Rotation and adduction occur rather late. The only discernible difference between species is in the crouching posture prior to acceleration for take off, with *A laniger* and *P. verreauxi* assuming a slightly deeper crouch, and *P. diadema* and *I. indri* exhibiting slightly more hip abduction.
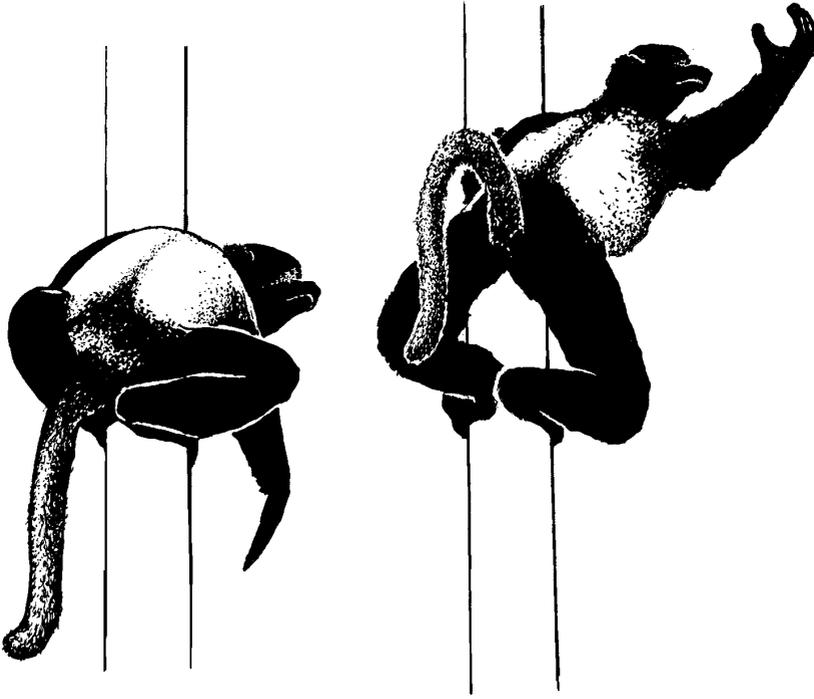
Figure 4. Take off of *Propithecus diadema* viewed from behind, drawn from videoimages. (A) Animal at the beginning of acceleration for take off. The thighs are abducted and externally rotated. (B) Midway through acceleration for take off. The knees are virtually pointing sideways; i.e., the thighs are rotated externally close to 90°.

Knee. In all four species, the knee joint is flexed to the smallest possible angle (leg opposed against thigh) before acceleration for take off and is fully extended at take off for longer jumps. In other words, the knee joint passes through its maximum range of flexion–extension. Shorter hops are performed without maximum extension. No consistent differences between species were observed.

Foot. The following quantitative data are based on a small number of take offs for the two sifaka species and *I. indri*. Qualitative descriptions are based on a more comprehensive sample. No obvious differences in foot positions or movements were observed among these species. Unfortunately, the video footage of the smallest indriid, *A. laniger* does not enable us to comment on foot movements with any confidence (i.e., no foot close-ups, insufficient film speed).

The foot in larger-bodied indriid leapers transmits the force generated by the animal to the substrate but is not used as a propulsive lever. It releases the grip around the support without contributing much to accelerating the body. In the majority of cases, the animals push off at the deep cleft between the first and second ray, that is in the midfoot region (Figure 5; Table 6). The metatarsals and phalanges II to V are positioned along the lateral aspect of the substrate, even on large-diameter supports, and the long axis of the digits is perpendicular or oblique to the substrate's long axis. Forceful plantarflexion, therefore, cannot produce a major force component in the direction of movement (Figure 5). In a smaller number of take offs
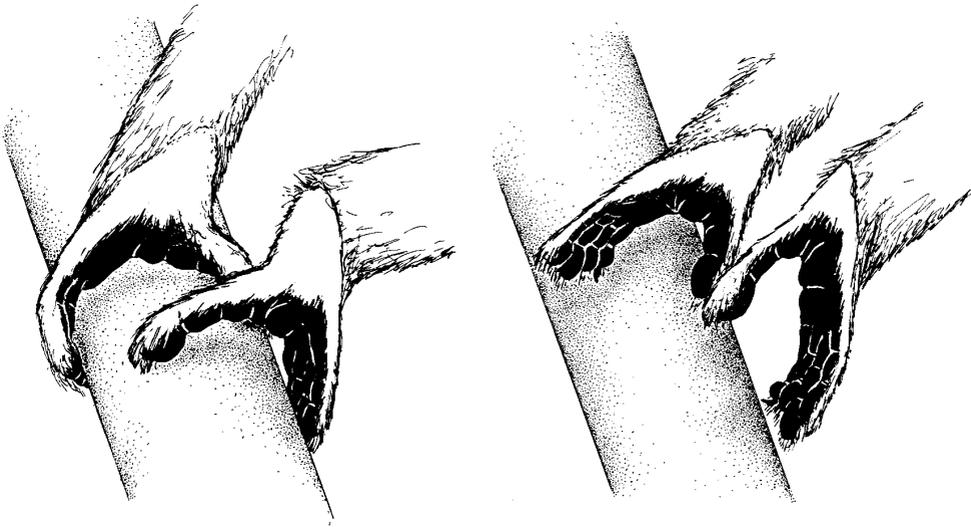
Figure 5. Close-up of *Propithecus verreauxi* feet at take off. The feet release the grip around the support with toes II–V coming off the lateral surface of the support.

Table 6   **Pedal push off point at take off**

Species	n	Midfoot*	Forefoot†
Propithecus verreauxi	22	14 (64%)	8 (36%)
Propithecus diadema	18	17 (94%)	1 (6%)
Indri indri	11	8 (73%)	3 (27%)
Test for interspecific differences‡		$P>0·05$	

*The push off contact is at the level of the cleft between the hallux and the lateral toes.
†Includes metatarsal or phalangeal levering off.
‡Row by column test of independence using the William's correction (Sokal & Rohlf, 1981).

from large diameter supports, the feet are positioned on the surface of the substrate facing the animal. In this situation the metatarsals and phalanges can and may actually contribute additional leverage (forefoot push offs, Table 6). Similarly, in take offs from horizontal or nearly horizontal substrates, where the foot is perpendicular to the substrate, the metatarsals often seem to function as levers. This explains the rather high number of forefoot push offs in *P. verreauxi*; as described earlier, this species frequently uses horizontal and oblique supports in Ampijoroa (see also Table 1).

The total range of sagittal plane movement at the ankle, intertarsal and metatarsophalangeal joints was estimated to be less than 90° in both *Propithecus* species and *I. indri*. At take off, the angle between the foot and the leg is still about 90–130° (based on 15 observations). Plantarflexion continues after take off. The greatest angular excursion takes place at the ankle joint. There is visible, though moderate, sagittal plane movement at either the metatarsophalangeal or midtarsal joints (because of their close proximity, this cannot be

Figure 6. Close-up of *Indri* feet during acceleration for take off. (A) The plantar surfaces of the hindfeet (which are covered with fur) are facing each other. (B) The hindfeet are partly everted. (C) The hindfeet are everted with the two plantar surfaces now facing almost straight downward. Printouts from video images.

Table 7   Arms and tail during acceleration for take off

Species	n	Arms* No	1	2	n	Tails† No	45°	90°
Avahi laniger	5	5 (100%)	—	—	6	4 (66%)	1 (17%)	1 (17%)
Propithecus verreauxi	67	10 (15%)	23 (34%)	34 (51%)	67	35 (52%)	12 (18%)	20 (30%)
Propithecus diadema	32	2 (6%)	30 (94%)	—	35	12 (34%)	4 (12%)	19 (54%)
Indri indri	36	—	28 (78%)	8 (22%)	‡			
Test for interspecific differences§		$P<0.01$				$P>0.05$		

*No=passive; 1=one arm is swung up and out; 2=both arms are swung up and out.
†No=no movement; 45°=tail is swung up to an angle of about 45° with the trunk; 90°=tail is swung up to about a right angle.
‡Indri has only a rudimentary tail, and its action was not scored.
§Row by column test of independence (Sokal & Rohlf, 1981).

distinguished on the videos). The heel does not contact the substrate at any point during acceleration for take off.

   Because the digits do not move against the substrate during most of acceleration for take off, adduction and rotation at the hip must be accompanied by movements of corresponding amplitude at some other joint within the hindlimb. Several close-ups for both *Propithecus* species and *I. indri* suggest that these movements take place within the foot. Figure 6 shows an example of a take off of *I. indri*. In the initial, crouched stages of acceleration for take off, the plantar surfaces of the two heels face each other, and the posterior projection of the heel is pointing medially [Figure 6(a)]. During acceleration for take off, the plantar surfaces of the heel are rotated so that they face almost straight downward, and the heel projects posteriorly [Figure 6(b), (c)]. This means that the hindfoot is everted during acceleration for take off. As the digits remain facing inward in order to continue grasping the support, hindfoot eversion must be accompanied by inversion of the forefoot relative to the hindfoot at the transverse tarsal joints.

Arms and tails
Larger-bodied indriid leapers (*Propithecus*, *Indri*) frequently swing one or both arms up and out during acceleration for take off. When both arms are used, one of them usually holds on to the substrate slightly longer, and is delayed in its rotating action (Figure 1). There are differences between species in arm activity during take off (Table 7). In the five take offs of *A. laniger* that could be analyzed in this respect, the arms were held passively and flexed in front of the trunk. In half of the cases *P. verreauxi* swings up both arms, whereas the larger-bodied *P. diadema* and

Table 8 Arms and tail while airborne

Species	Arms			Tail		
	n	Yes	No	*n*	Yes	No
Propithecus verreauxi	19	18 (95%)	1 (5%)	21	20 (95%)	1 (5%)
Propithecus diadema	4	4 (100%)	—	5	5 (100%)	—
Indri indri	4	4 (100%)	—	—	—	—
Test for interspecific differences*		P>0·05			P>0·05	

"Yes" and "no" categories indicate frequencies of the arms being swung forward and downward and the tail being swung upward simultaneously with the hindlimbs being brought forward into landing position. Indri has only a rudimentary tail, and its action was not scored.

*Row by column test of independence (Sokal & Rohlf, 1981).

I. indri usually swing only one arm up and out. This difference suggests that *P. verreauxi* uses the arm movement to enhance push off force whereas *P. diadema* and *I. indri* enhance body rotation about the longitudinal axis (see discussion).

The arms are almost invariably used by both sifaka species and *I. indri* to counteract the rotating moment of the forward swinging hindlimbs while the animals are airborne (Table 8). Unfortunately, data for *A. laniger* are not available.

During acceleration for take off, the tail (except for *I. indri* which has only a rudimentary tail) is swung upward in about half of all observed cases (Table 7). While airborne, the tail is moving upward simultaneously with the hindlimbs moving into landing position (Table 8). In two leaps of *P. verreauxi*, the rotation of the body about the long axis was still in progress when the hindlimbs were brought forward. The body was oriented laterally to the direction of movement. In this position, rotation about a craniocaudal instead of a transverse axis is required to direct the hindlimbs towards the target support. In both cases, the tail was moved in a full circle to make the trunk rotate in opposite direction. This underscores the potential importance of tail movements for body repositioning.

Discussion

Indriid leaping kinematics and hindlimb design

The data presented here are the first kinematic information about large-bodied indriid leapers that provide hard evidence in support of the long-suspected dichotomy in leaping behavior between galagos and tarsiers on the one hand and indriids on the other. Based solely on morphological evidence, indriids were described as long-thighed jumpers (Jouffroy & Gasc, 1974; Jouffroy & Lessertisseur, 1979) and thigh-powered jumpers (Gebo & Dagosto, 1988). This was based on the dominance of the proximal segment within the hindlimb and the lack of obvious leaping adaptations in the foot. Tarsiers and galagos, on the other hand, were described as tarsifulcrumators (Morton, 1924), long-tarsal jumpers (Jouffroy & Gasc, 1974; Jouffroy & Lessertisseur, 1979) or foot-powered jumpers (Gebo & Dagosto, 1988), characterized by tarsal elongation and a comparatively short femur. Kinematic data on galagos have confirmed this latter locomotor pattern, demonstrating the use of the foot in propelling the body (Günther, 1989), whereas the indriid pattern remained hypothetical until now.

Hindlimb kinematics substantiate the importance of the most proximal joint in propulsion for indriid primates. Angular excursions at the hip are increased by assuming deep crouching

Table 9   **Hip flexion in tarsiers and galagos**

	n	Knee position*		
Species	Ventral	Midaxillary	Dorsal	
Tarsius syrichta	21	12 (57%)	9 (43%)	0
Galago moholi	20	4 (20%)	12 (60%)	4 (20%)

*Knee position before acceleration for take off is scored relative to the midaxillary line.

positions in which the trunk is lowered between the abducted limbs prior to acceleration. A similar behavior has been described by Günther (1989; Günther *et al.*, 1991) for *Lemur catta* taking off from a horizontal platform. He never observed this same behavior in two *Galago* species (*Galago moholi*, *Galago garnettii*), and minimum hip joint angles of flexion for *Tarsius bancanus* are also well above zero (Niemitz, 1984a). Direct comparison of these observations with our own data is, however, complicated by the fact that the comparative small-bodied sample is restricted to horizontal platform take offs in laboratory settings. We therefore analyzed additional take offs of *G. moholi* and *Tarsius syrichta* from vertical supports with the same methods used for the indriid sample. Animals were filmed in seminatural cage settings at the Duke University Primate Center. The data suggest that *G. moholi* accelerates on vertical supports from a more deeply crouched position than when taking off from horizontal platforms (Table 9). The degree of hip flexion for both species overlaps with that of the indriid leapers. A row by column test, however, reveals the average hip flexion angle to be significantly different from that of the indriid primates ($P<0.01$). The available evidence strongly suggests that indriids are characterized by greater joint excursions at the hip than are galagos and tarsiers.

The ankle and intertarsal joints show just the opposite pattern. Sagittal plane action is very limited in the indriids, with the long axis of the foot rarely aligned with the take off trajectory. Angular excursions at both these joints combined often does not exceed 90°. Günther (1989), on the other hand, reports angular excursions of 135° at the ankle joint for *G. moholi* and 100° for *G. garnetti*, plus 56 and 43° at the intertarsal joints, respectively (mean values for several leaps).

Our data on indriid leapers confirm the notion that they practice a jumping style that emphasizes proximal joint motions, and this finding matches their characteristic hindlimb proportions, with the proximal segment being elongated (Jouffroy & Lessertisseur, 1979; Anemone, 1993). Great angular excursion translates most effectively into long acceleration distance when it is coupled with increased segment length.

The foot of indriid primates is also long, but it is designed more for grasping than for propulsion (Walker, 1974; Gebo & Dagosto, 1988; Gebo, 1993). Unlike in tarsifulcrumating tarsiers and galagos, it is the forefoot that is elongated in indriids, whereas mid- and hindfoot are comparatively short (Jouffroy & Lessertisseur, 1979). Few leaping specializations are found in the ankle joint of indriids (Gebo & Dagosto, 1988), where most of the limited sagittal plane movements take place. The foot itself is characterized by a high degree of rotatory mobility (Gebo & Dagosto, 1988). Hindfoot eversion during acceleration for take off with the grasping forefoot fixed to the substrate (see above) requires considerable rotation within the foot and explains its midtarsal rotatory mobility. Indriids can be characterized as tarsirotators rather

than tarsifulcrumators. Data on foot mobility gained from manipulating cadaver feet confirm this notion. Ranges of plantar- and dorsiflexion at the ankle and transverse tarsal joint are considerably larger in galagos and tarsiers than in indriids (represented by *Propithecus*), whereas ranges of inversion and eversion are greater in the indriid (Gebo, 1993).

All vertical clingers and leapers share a number of leaping specializations in femoral shape (Anemone, 1990 and references therein), but femoral head shape divides them into two distinct groups: galagos and tarsiers with cylindrical femoral heads, and indriids with more spherical heads (Napier & Walker, 1967; Grand & Lorenz, 1968; Walker, 1974; Anemone, 1990, 1993; Dagosto & Schmid, 1996). The cylindrical shape with an articular expansion on the posterior aspect has been interpreted by Anemone (1990, 1993) as an adaptation to accommodate flexed, abducted, and externally rotated thigh postures. The indriid hip morphology with a shallow acetabulum and a spherical femoral head was explained to accommodate mobility for the wide range of suspensory postures exhibited by these animals (Godfrey, 1988). Our kinematic data, however, suggest that indriids (during acceleration for take off) assume highly abducted and externally rotated thigh postures, and comparative evidence suggests that the degree of abduction and rotation may even exceed the ranges of galagos and tarsiers. Günther (1989) reports rather moderate abduction angles of 25° for *Galago senegalensis*, and Jouffroy & Günther (1985) describe maximum abduction angles of 18° during sitting postures on a horizontal plate for these animals. Angles between 30 and 40° were measured for five take offs from vertical supports of *G. moholi* filmed in posterior view at the Duke University Primate Center. These angles are smaller than our own measurements on indriids. Individual cine-X-ray frames published by Jouffroy & Gasc (1974), on the other hand, seem to indicate a greater degree of hip abduction for *Galago alleni* during the second half of the take off acceleration.

Manipulation of skeletal specimens of *G. senegalensis* and *P. verreauxi* also suggests that the indriid hip morphology allows highly abducted limb postures in flexed and extended positions. With the fovea capitis within the inner articular margins of the acetabular fossa (Jenkins & Camazine, 1977), the sifaka femur could be abducted to an angle of about 70°, and the *Galago* femur only to an angle of 45°. In an unembalmed cadaver of *P. verreauxi* the flexed thigh was easily manipulated into abduction angles of up to 90°. X-rays reveal significant articular contacts at these abducted and flexed limb positions (Figure 7).

Although the posterior expansion of the femoral head in small-bodied leapers provides articular surface for abducted postures (Anemone, 1990), the indriid hip design clearly allows even more abduction, and the kinematic evidence seems to suggest that these animals go through more abducted thigh postures when taking off than do galagos and tarsiers. The less mobile cylindrical joint shape of these species may be better interpreted as an adaptation for greater stability required to accommodate the relatively higher locomotor forces that characterize these smaller-bodied leapers (Günther, 1989; Demes & Günther, 1989; Demes *et al.*, 1995).

Body size and dynamic similarity
The theory of dynamic similarity predicts that with increasing body size animals adjust locomotor parameters to compensate for the increase in weight-related musculoskeletal forces (Hill, 1950; Alexander, 1976; Alexander & Jayes, 1983; Biewener, 1983; Rubin & Lanyon, 1984). In broad scale comparisons of quadrupedal species, its explanatory power for size-related variation in locomotor kinematics and kinetics has been repeatedly demonstrated (e.g., McMahon, 1984; Alexander & Jayes, 1983). Bennet-Clark (1977) identified the major

Figure 7. X-ray of the hip of a cadaver of *Propithecus verreauxi* with the thigh in an abducted and flexed position. Note the overlapping joint surfaces of the femoral head and the acetabulum.

mechanical constraints of leaping at small body size as being the limited time available for acceleration, and Demes & Günther (1989) hypothesized that the more limited force available to accelerate a given unit of body mass constrains leaping at large body size. Small-bodied leapers must accelerate over small distances and show adaptations in body proportions and movement patterns that maximize the distance and, hence, length of time for propulsion. Because of their absolutely greater dimensions, larger-bodied leapers can accelerate over longer periods of time. However, as muscle force increases as a function of area and weight force is proportional to volume, large-bodied leapers have less muscle force per unit mass to be accelerated. Body proportions and locomotor patterns are, therefore, adaptive that reduce high joint movements, especially at distal joints that are extended against the resistance of the greatest proportion of weight force. The kinematic predictions derived from the concept of dynamic similarity as applied to leaping include: with increasing size a general reduction in angular excursion of the hindlimb joints and greater angular excursions at proximal *vs.* distal hindlimb joints, and acceleration for take off over a longer period of time. For a diverse sample of primate "leapers" (two galago species, *L. catta* and *Homo sapiens*) these patterns were confirmed (Demes & Günther, 1989).

Indriid primates are an ideal study group to test allometric trends because they exhibit a wide range of body sizes and they are phylogenetically closely related. Surprisingly little size-related variation was found in leaping styles from the smallest species, *Avahi*, to the largest

species, *Indri*. With the exception of the hip joint there is no indication in our data that the larger species sacrifice angular excursions to avoid acute and dynamically challenging joint angles. At the hip, the two smaller species start acceleration for take off at smaller angles and, consequently, go through greater total angular excursions. Knee and ankle joint kinematics are very similar for the three species. When compared with other prosimian leapers, the total size range is increased considerably at the lower end of the scale. As pointed out above, a major difference between indriid leapers on the one hand and galagos and tarsiers on the other is the greater emphasis of hip joint movements in the former and emphasis on ankle joint movements in the latter species—which has been predicted (Demes & Günther, 1989).

As angular excursions at the major hindlimb joints do not differ much between indriid species and absolute hindlimb length increases with body size, it is not surprising that acceleration time increases with body size. This increase in time over which propulsive force is exerted concurs with allometric theory and also characterizes non-indriid leapers (Demes & Günther, 1989). It is interesting to note, however, that acceleration time for *A. laniger* is almost identical to that of the much smaller *G. moholi* taking off from a horizontal platform (Günther, 1989). Absolute hindlimb length in the indriid is only about two times that of the galago despite the much larger difference in body weight (unpublished data). It appears that the small-bodied leapers possess disproportionately elongated hindlimbs in order to maximize the time (and distance) required to generate sufficient impulse for take off (Bennet-Clark, 1977; Demes & Günther, 1989). In addition, *G. moholi* shows much more ankle extension and also extends at the intertarsal joints when accelerating (Günther, 1989; see also above). The overall acceleration distance of the smaller galago may, therefore, come close to that of the *Avahi*.

It has been shown previously (Demes *et al.*, 1991) that long bone cross-sectional dimensions of indriid primates scale close to isometry and it was hypothesized that changes in locomotor performance rather than bone robusticity compensate for the weight-related increase in forces and moments. Our current data suggest that indriids do not reduce load arm lengths with increasing size by avoiding acute joint angles. However, the longer acceleration times of the larger-bodied animals are reason enough to suspect that the larger-bodied species accelerate with more moderate peak forces (Demes & Günther, 1989). In addition, although load arm lengths are not modified behaviorally, the negative allometry of hindlimb length in indriids (Jungers, 1985) does reduce the relative magnitude of moments in the larger-bodied species.

Preparatory countermovements
The potential performance benefits of countermovements, routinely performed by indriid leapers, include muscle pre-tensing, prolongation of the propulsive phase, utilization of elastic strain energy, and providing an initial propulsive force (Komi & Bosco, 1987; Hochmuth, 1984; Anderson & Pandy, 1993; Zajac, 1993; Voigt *et al.*, 1995). Mathematical modeling of human and prosimian jumping also suggests that greater heights are achieved by counter-movement jumps over squatting jumps (Alexander, 1995). It has been demonstrated in humans that drop jumps from small heights enhance performance over squatting jumps (Komi & Bosco, 1987). The initial hop represents a preparatory movement mechanically similar to drop jumps. In the absence of experimental data, the ultimate purpose of preparatory movements in indriids remains open to speculation. The size-related difference in the type of countermovement performed matches predictions related to the decrease in ratio of muscle force available for acceleration to the body mass that has to be accelerated (Demes & Günther, 1989). Larger-bodied species are likely to have relatively less force, and may therefore use the most efficient bounce more frequently.

Table 10   **Tail length of vertical clingers and leapers**

Species	Head and body length (mm)	Tail length (mm)	Ratio
*Tarsius bancanus**	129	217 (n=82)	1·68
Galago senegalensis†	161	235 (n=20)	1·46
Avahi laniger†	315	392 (n=2)	1·24
Propithecus verreauxi‡	440	502 (n=22)	1·14
Propithecus diadema‡	486	455 (n=9)	0·94
Indri indri†	700	30 (n=1)	0·04

*Niemitz, 1984b; †Napier & Napier, 1967; ‡Simons, 1988.

Take off angles

Although take off angles are centered around the optimum 45° angle for all species, the great range of angles seems to suggest that they are determined at least in part by the height of the target landing spot. Several species of vertical clingers and leapers filmed at the Duke Primate Center jumped from an instrumented force pole at more predictable angles of around 45° (Demes *et al.*, 1995, 1996). In this laboratory set up, the vertical dimension of the activity range was much more restricted in comparison to the wild (the take off and landing section of the pole was only 2 m long). A similarly narrow range of take off trajectories was reported by Treff (1970) for *G. moholi* leaps in an experimental setting. Optimizing the take off angles may also become more influential in long leaps that are closer to the performance limits of the animals. Our field data do not include information on leaping distances to evaluate this hypothesis. Laboratory data by Crompton *et al.* (1993) demonstrate that *G. moholi* takes off using the optimum trajectory no matter what distance it covers, whereas *G. garnettii* and three species of cheirogaleids approach the 45° inclination only at longer distance leaps.

Arms and tails

Whereas the hindlimbs are clearly the major force in delivering the propulsive thrust in indriid take offs, the forelimbs and the tail play an important role in body positioning during acceleration, and they have an obvious influence on midflight kinematics. The potential effects of arm and tail movements are a function of the weights of these segments relative to the rest of the body (Peters & Preuschoft, 1984; Demes & Günther, 1989; Demes, 1991), and these weight relations scale allometrically with size. Relative weight of the upper limb increases with increasing body size in a broad sample of 20 primate species including prosimians, cercopithecoids and hominoids (Demes, 1991). The forelimb of *G. senegalensis* represents 3·8% of total body mass (Grand, 1977), whereas that of *P. verreauxi* is 5·2% (unpublished data on one female individual following methods of Grand, 1977). Tail weights are not readily available in the literature. However, if tail length is taken as an indicator of tail weight, it is quite obvious that the tail is reduced with size within indriids as well as within vertical clingers and leapers (Table 10). Similarly, Ravosa *et al.* (1993) demonstrate that *P. diadema* has a relatively shorter tail than *P. verreauxi* and *P. tattersalli*. Peters & Preuschoft (1984) report a relative tail weight of 3·9% for *T. bancanus*, and the tail of a female *P. verreauxi* was recorded to be 2·1% of body weight (unpublished data). Based on these proportions it can be expected that larger-bodied leapers rely on their forelimbs, and smaller-bodied leapers use their tails for body position adjustments.

During acceleration for take off, sifakas and indris swing one or both arms upward and outward, whereas *Avahi* keeps its arms tucked into the chest, similar to what has been described for tarsiers and galagos; in these species, the arms are involved only in very powerful long distance leaps (Hall-Craggs, 1965; Charles-Dominique & Bearder, 1979; Niemitz, 1984a; Jouffroy & Günther, 1985; Günther *et al.*, 1991). Biomechanically, the profit of such arm movements is an increase in the push off force, and, if employed asymmetrically, they can also contribute to angular momentum about the body's long axis (Hochmuth, 1984). Because of the greater weight, forelimb movements may be sufficiently beneficial on a routine basis only for the larger-bodied indriid leapers.

Dorsiflexion of the tail during acceleration for take off was described by Günther (1989; Günther *et al.*, 1991) for *G. senegalensis*, and its action was attributed to a need to counterbalance the tendency of the center of gravity to flex at the hip joint. Dorsiflexion of the tail was also observed in most take offs of the indriid leapers. No size effect is, therefore, apparent in the use of the tail during acceleration for take off, a conclusion that is also supported by the fact that the *I. indri* and *P. diadema* are virtually identical in body size (Glander *et al.*, 1992; Mittermeier *et al.*, 1994) but differ greatly in tail length.

When airborne, small-bodied prosimian leapers use their tails to initiate rotation of the body around a transverse axis while the arms are held passively in front of the chest (Hall-Craggs, 1965; Charles-Dominique & Bearder, 1979; Peters & Preuschoft, 1984; Niemitz, 1984a). Tarsiers and galagos assume a ball-shape to minimize inertia, and the counterbalancing angular momentum necessary to bring their hindlimbs forward is gained by rapidly swinging their tails up (Oxnard, 1983; Peters & Preuschoft, 1984). Indriid primates, as far as they have tails, also swing them up while their hindlimbs are brought forward. In addition, and unlike tarsiers and galagos, they also invariably use their arms, which are flexed and adducted from an originally extended and spread out position. Dual action of arms and tails has also been described by Dunbar (1988) for *L. catta*.

In summary, while tail use during leaping behaviors seems to be independent from body size, the use of the forelimbs during acceleration for take off and in the aerial phase of the leap is restricted to larger-bodied leapers. Forelimb use may become indispensable with increasing size to augment the more limited effects of movements of a tail decreasing in length and weight. Increased forelimb weight also makes their action more beneficial.

Conclusions

(1) Indriid leaping is characterized by a wide range of movements at the hip joint, where extension is accompanied by a considerable amount of adduction and medial rotation during acceleration for take off. The spherical femoral head and shallow acetabulum are correlated with this mobility.

(2) The indriid foot is rarely used for propulsion; it accommodates the extensive hip movements by large amounts of hindfoot eversion and accompanied inversion of the forefoot at the transverse tarsal joints. Indriids are "tarsirotators" and not "tarsifulcrumators".

(3) Take off angles in the wild are variable but centered around the optimal 45° angle; they seem to be influenced by the height of the landing target as much as by optimization criteria.

(4) Preparatory countermovements are used routinely to enhance leaping performance, and these bounces are seen more predictably in the largest species.

(5) Other size-related differences in hindlimb kinematics are minimal within indriid primates despite the considerable size range represented (almost one order of magnitude). Differences

between indriid hindlimb use and that of smaller-bodied galagos and tarsiers do exist and more or less concur with dynamic similarity. Acceleration times increase with size within indriids as predicted by dynamic similarity.

(6) Forelimb kinematics are clearly influenced by body size both within indriids as well as within other vertical clingers and leapers. Larger-bodied species with relatively heavier forelimbs use them to augment force during acceleration for take off and to initiate body rotations. Smaller-bodied species appear to rely exclusively on their tails for these purposes.

Acknowledgements

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