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A Consideration of Leaping Locomotion as a Means of Predator Avoidance in Prosimian Primates

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Introduction

Predator pressure is normally very difficult to assess, and most reports tend to be anecdotal. However, it has been estimated that an annual predation rate of 25% may apply to *Microcebus* populations (Goodman et al., 1993). Such a rate, albeit for a particularly small prosimian, implies strong selective pressure in favor of adaptations that reduce predation, and it seems reasonable to assess adaptations with predation in mind. Predator avoidance by vigilance is usually seen as an attribute of social foragers (see, e.g., Terborgh & Janson, 1986), to which category many of the Lemuridae, and arguably some Indriidae and Lepilemuridae, belong. However, the small body size and nocturnality of those prosimians described as "solitary foragers" are often regarded as facilitating alternative predator avoidance strategy, crypsis (e.g., Clutton-Brock & Harvey, 1977; Stanford, 2002).

A rather more obvious and striking specialization of prosimians, however, is their proclivity for leaping. In this paper we suggest that rather than crypsis, leaping is actually the primary predator-avoidance device in prosimian primates classed as solitary foragers, and indeed may play as important a role as vigilance in many more gregarious taxa. Equally, while no single selective pressure is likely to be uniquely responsible for the widespread adoption of leaping locomotion by prosimian primates, the balance of evidence suggests that as in many non-primate leapers, leaping has indeed been adopted *primarily and originally* as a predator-avoidance device.

Leaping in Prosimians

Among vertebrates, it is the prosimian primates that display the most outstanding saltatory performances. *Galago moholi*, for example, leap distances and heights which are the greatest multiple of body length found in any vertebrate: horizontal leaps of 4 m and height gains of over 2 m may be achieved. Leaping is not only well-developed in prosimians, but it is nearly ubiquitous. In 22 genera of living prosimians, only four (*Nycticebus*, *Loris*, *Perodicticus*, and *Arctocebus*) do not leap at all. All those that do leap use leaping as a substantial element of their locomotor repertoire (reviewed in Walker, 1979; Oxnard et al., 1989). The four exceptions are all tailless, with sub-equal limb lengths, rather than the hindlimb-dominated intermembral indices which Napier and Walker (1967) famously identified as a marker of the locomotor category, vertical clinging and leaping. The four are supposedly all relatively slow moving and have adaptations such as a *rete mirabile*, an enhanced vascular network in the muscles, which permits muscles to remain in contracted state for extended periods. Their predatory behavior has been described as "stealthy" (Walker, 1969): slow movement, it was claimed, that is used to approach prey without disturbing the surrounding vegetation. Stealth may, of course, serve the needs of predator avoidance as well as it may those of predation, and indeed Charles-Dominique (1971) has argued that the slow locomotion of *Loris*, *Arctocebus*, and *Perodicticus* is actually an adaptation for predator-avoidance by crypsis. Walker (1969) contrasted the stealthy strategy of lorises with that of their relatives, the galagos, where speed of predatory movement is served by leaping. Although an apposite characterization of the behavior of *G. alleni* (Charles-Dominique, 1971) and *G. moholi* (Crompton, 1984), this adaptation is even more characteristic of tarsiers, which have recruited the leap as the basis of the predatory pounce from perches on vertical sapling-trunks near ground level (Fogden, 1974; Niemitz, 1979, 1984a; Crompton, 1989; Crompton & Andau, 1986; Oxnard et al., 1989; Jablonski & Crompton, 1994).

Thus, for some species at least (as in the case of the tarsier's predatory pounce) there might be an argument for linking prosimian leaping to hunting (i.e., engaging in, rather than avoiding, predation); but of course many prosimian leapers such as indriids, gentle and sportive lemurs, and ringtail lemurs are not primarily, or even substantially animalivorous (reviewed in, e.g., Hladik, 1979).

(NB: To link "stealth" necessarily to slow speed seems increasingly inappropriate. Anna Nekaris (pers. comm.) has since discovered that in the wild, the 130-g red loris can reach 1.29 m/s, an absolute speed well within the range of human walking speeds. Nekaris (2005) thus describes the Mysore loris's (*Loris lydekkerianus*) locomotion as "stealthy but swift." At least the pygmy slow loris may also be capable of quite high speeds, and the applicability of both Walker's (1969) and Charles-Dominique's (1971) descriptions may thus be quite limited.)

Kinetics and Kinematics of Leaping

Leaping style and leaping mechanism

Three categories of leaping "style" (see e.g., Oxnard et al., 1989) have been defined: static leaping, in which the animal pauses before making a leap; running leaping, in which the animal makes a transition from a run to a leap; and ricochetal leaping, in which the animal links together a succession of individual leaps with no pause or strides between each individual leap. In addition to these *outcome* groupings there are categorizations depending on the *mechanism* (see, e.g., Alexander, 2003) used to generate the power required for leaping: squat leaping, where muscle contraction alone is the motive force; countermovement leaping, in which a previous movement is used to store elastic energy that is released during take-off; catapult leaping, in which a locking mechanism is used to allow muscles slowly to bring about maximum tension, which can then be quickly released during take-off; and vaulting leaping, where a rigid strut is used to alter the direction of movement of the center of mass. All these mechanisms are potentially applicable to all the leap styles (with the probable exception of vaulting combined with ricochetal leaping), but it is most likely that the squat, catapult, and countermovement mechanisms are all used to perform static leaps. Countermovements are also involved in ricochetal leaping. It is striking in the context of a possible predator-avoidance role for leaping that the commonest outcome category in most primates (let alone prosimians), running leaping, is almost certainly brought about by vaulting, where an intrinsic element of change in the direction of movement exists; and this change is of course *sudden.*

While large animals benefit from the absolutely greater length of their limbs, which allows them to apply smaller forces over a longer take-off period, scaling effects also suggest that muscle physiological cross-sectional area will be larger in them compared to body mass in small mammals (see e.g., Demes & Günther 1989), so that even though the reduced take-off distance available to small animals necessitates higher power outputs, relatively more power is indeed available to them. However, Hall-Craggs (1962) noted that the calculated required power output for an observed maximum vertical leap of *Galago senegalensis*, gaining 2.25 m in height, is well in excess of the maximum capacity of vertebrate muscle (Bennet-Clark, 1977), which implies the existence of some means of power amplification. Aerts (1998) made a dynamic analysis of leaping in the lesser galago which lead him to suggest that the required power amplification could be obtained by a sequential recruitment of countermovement, catapult, and squat “with compliant tendons” (Alexander, 1995) mechanisms.

Leaping as a specialization

While leaping always tends to require a higher degree of musculoskeletal specialization than cyclic locomotor modes, not all prosimian leapers are equally specialized. Indeed, they may usefully be divided into specialist and non-specialist leapers. This is not just a matter of the percentage of movements that are leaps or the contribution to each kilometer of travel that is made up by leaping. Although arm swinging is used to extend a series of leaps by sifakas (author Crompton, pers. obs.), it is almost certain that all prosimian leapers power the leap primarily with the hindlimb. Specialist prosimian leapers, indeed, tend both to take off from, and to land on, their hindlimbs. This both maximizes the distance over which the body center of mass can be accelerated before losing contact with the ground and the distance over which it can be decelerated on landing. This in turn implies that specialist leapers require some mechanism for changing body posture in mid-flight. This is accomplished by a tail-flick in *Galago* and *Tarsius.* Given these animals’ small body size, the tail-flick presumably must act by changing the rotational inertia of the body, not by means of air resistance (Peters & Preuschoft, 1984). Mid-flight rotation is, however, accomplished by countermovements of the forelimbs in the large-bodied *Indri* and *Propithecus* (Preuschoft et al., 1998). Whether the use of the arms in these large species is a consequence of the greater air resistance they encounter (Bennet-Clark, 1977) is unclear, but air resistance may be exploited by indriids to increase maximum leap length, since loose skin under the abducted arms might provide a "gliding" effect, albeit at the expense of reducing speed. *Indri*, of course, lacks a tail; but *Propithecus*' tail appears simply to trail the body during leaps. Tail-flicks, and forelimb countermovements can alter orientation during flight. However, only the use of air resistance permits change in direction and/or leap length in mid-flight.

Generalists tend to land forelimb first, which at least in larger species may limit the force they can afford to experience on landing, and may thus also limit leap speed or distance (Oxnard et al., 1989). Choice of a compliant substrate as a landing target will, however, negate this problem, albeit at the cost of increased disturbance to the surrounding vegetation. Thus, for example, while Demes et al. (2005) found that the *Lemur catta* they studied tended to land hindlimb first, their *Eulemur* subjects landed forelimb first. In addition, *Eulemur* forelimb forces on landing were greater than hindlimb forces, although hindlimb forces on take-off were larger still.

Leaping and efficiency of transport

From basic physical principles it has been established that leaping locomotion is not in itself a very efficient way of moving around (Walton & Anderson, 1988). Except for ricochetal leaping, where leaps follow immediately upon each other at a stable resonant frequency, there is little or no possibility of the primate conserving energy between one leap and the next. Energy savings in ricochetal leaping may be served by elastic recoil of tendon and ligament and elastic units in muscles, stretched during landing, to help power the next leap. (There will of course be ecological situations where leaping remains the most efficient locomotor option: e.g., when crossing between trees, where the alternative to leaping from one canopy to the next may be to climb down one trunk and up the next.)

Leaping and musculoskeletal load

Leaping is also associated with high ground reaction forces compared to quadrupedalism (Günther et al., 1991; Demes et al., 1999) and behaviors that result in large forces are likely to influence musculoskeletal morphology (Alexander, 1981). As we have seen, the scale of forces required to be exerted during take-off varies with body size, so that Demes and colleagues (1999) give values of hindlimb take-off force of thirteen times body mass in *G. moholi*, but nine times body mass in *P. verreauxi*. The more striking contrast was, however, with quadrupeds of equivalent size, where forces are only just over twice body mass. Thus, leaping is thus not only energetically expensive as a means of transport compared to quadrupedalism, but also incurs higher musculoskeletal loads, and thus requires a greater degree of musculoskeletal specialization.

Leaping and transport speed

In contrast to popular expectation, leaping is not a particularly fast method of travel. Günther et al. (1991) recorded maximum velocities at take-off of 5.1 m/s for *G. moholi* leaping from a forceplate, and noted that this compares unfavorably to velocities of 15 m/s or more, which may be attained over short distances by a galloping, cursorial quadruped. The velocity Günther recorded is slightly greater than the 4.4 m/s required by leapers to attain a height of 1 m, irrespective of size (according to Bennet-Clark, 1977). As *G. moholi* (atleast according to Hall-Craggs, 1964, 1965) can gain 2.25 m in a leap, 5.1 m/s must be an underestimate of actual velocity maxima (although doubling vertical take-off velocity would quadruple height gain (Bennet-Clark, 1977). However, under natural conditions, Crompton recorded only a single record of a 2 m estimated height gain and only 39 of an estimated height gain of over 1 m in 2786 leaps by *G. moholi*. For *Tarsius bancanus* he recorded a maximum estimated height gain of 1.5 m, and only eight records of leaps over a 1 m height gain (of a total 1425 observed leaps). These field data tend to suggest that a take-off velocity of 5.1 m/s (Günther et al., 1991) is not substantially less than actual maximum velocities. Moreover, even anatomically specialized leapers do not often attain a velocity of 4.4 m/s (see Bennet-Clarke, 1977) in nature. Thus, most leaping occurs at ground speeds well under a third of the maximum speeds attained by cursorial quadrupeds, and actually rather closer to the speeds reached in arboreal quadrupedalism by *Loris*.

Since leaping is a ballistic action, we can readily derive predicted performances under different conditions. The ratio of distance travelled to force exerted at take-off varies with take-off angle and in-flight trajectory. Flight time is also dependent on trajectory, and the relative heights of the initial and terminal supports also need to be taken into consideration. Figures 6.1–6.3 show these relationships, and the equations used to derive these curves are given in Appendix 1, so that they may be used to analyze field data.

Figure 6.1 shows the mechanical energy cost of a leap for a set of take-off angles given the relative heights of the initial and terminal support (labeled "slope") for a 1 kg animal leaping 1 m. Figure 6.2 shows the flight time for a range of take-off angles and differing relative heights of initial and terminal supports ("slope"), again for a 1 m/s take-off velocity (the range for any combination of these values are given for equivalent values in Figure 6.3). Flight times for different take-off velocities are simple multiples, so the flight time for a speed of 2 ms would be twice the value given, for 4 ms it is 4 times the value, etc.). Figure 6.3 shows the range of a leap for a set of take-off angles and "slopes" for a 1 m/s take-off velocity. The range distance shown is the length of a line drawn from start to endpoint; the horizontal distance can be obtained by multiplying by the cosine of the "slope"

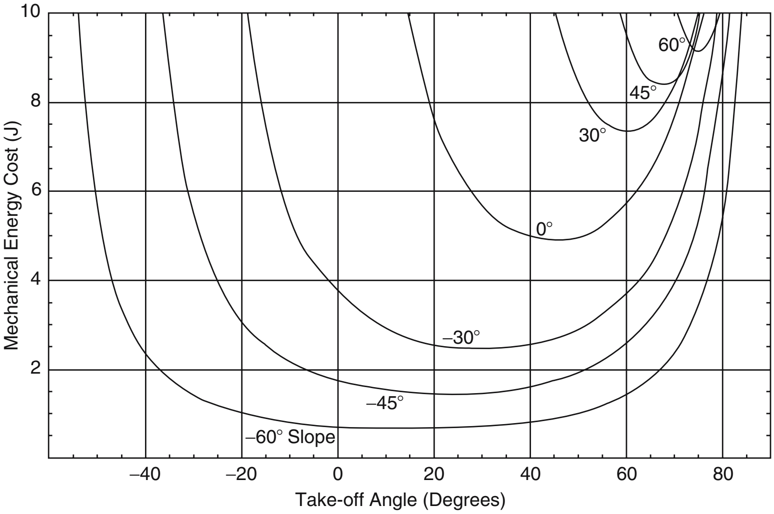

FIGURE 6.1. Mechanical energy cost of a leap for a set of take-off angles and relative heights of initial and terminal supports (slopes) for a 1 kg animal leaping a distance of 1 m

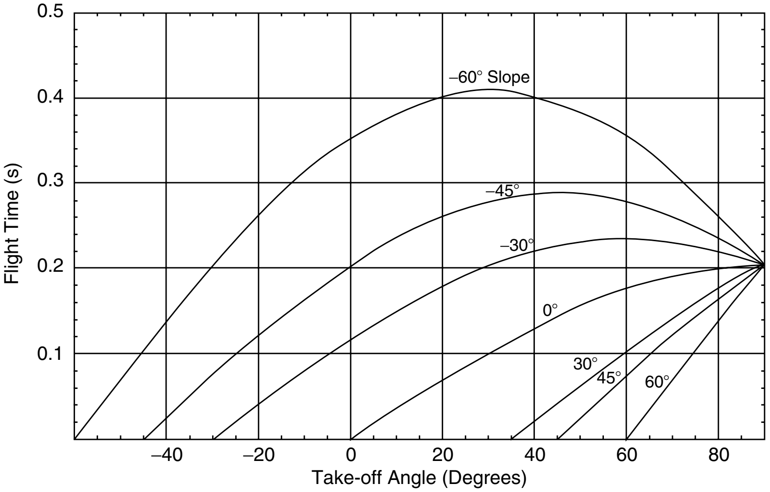

FIGURE 6.2. Flight time for a set of take-off angles and relative heights of initial and terminal supports (slopes) for a 1 ms take-off velocity

angle. Range depends on the square of the velocity, so range quadruples for twice the speed, is sixteen times greater for four times the speed, etc.

For any given combination of support heights, there is thus a take-off angle that will maximize travel distance (or equally minimize the energetic cost of travel). For level leaps at a take-off angle of 45°, distance covered for a given take-off

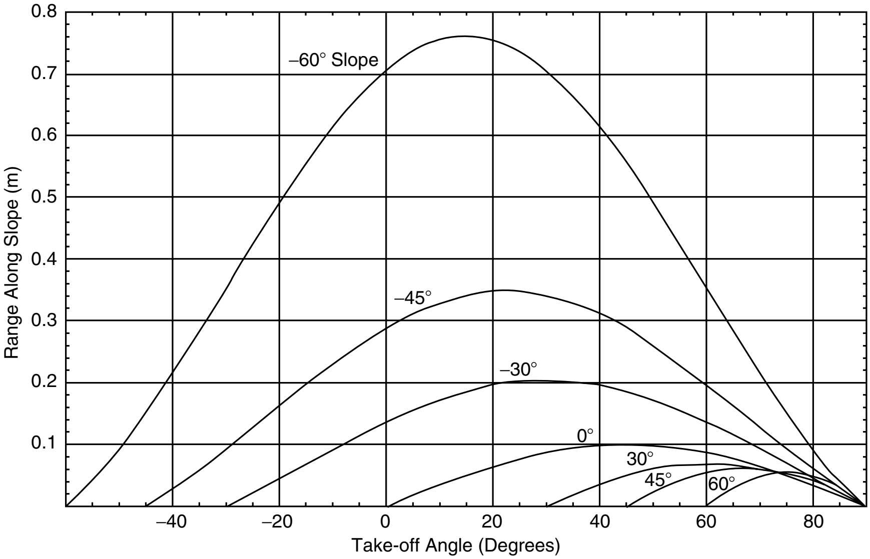

FIGURE 6.3. Range of a leap for a set of take-off angles and relative heights of initial and terminal supports (slopes) for a 1 ms take-off velocity. The range is measured along the slope

force is maximized, but such a leap is relatively slow. By contrast, a low, 20° take-off angle gives lowest costs for a 60° descent, while a take-off angle around 75° is required for maximum efficiency in a 60° ascent. Flatter trajectories cover less distance for the same take-off force, but less time is spent in the air. Very low take-off angles, while minimizing flight time, are always energetically expensive. While, in general, short flight times require low take-off angles, for downward leaps the longest flight times occur with moderate take-off angles. Leaping upward, however, is clearly much more expensive than leaping downward.

Perhaps surprisingly, Crompton et al. (1993) found that of five prosimian leapers studied in the laboratory, only the most anatomically specialized, *G. moholi*, habitually used the ballistically optimum take-off angle' 45°' at all leap lengths, in level leaps, although the other species tended to use this angle more often as leap distances approached the maximum they performed. This would seem to suggest that most prosimians opt for speed rather than distance in their leaping, or cannot readily adopt an appropriate body posture for a high-angled take-off, as discussed below. Demes et al. (1999) showed that "specialist" leapers, such as the indriids, exert relatively lower take-off and landing forces than less specialized leapers such as *G. garnetti*. Take-off force did not increase with distance (within the limited range of leap distances the authors could examine). In a study of leaping forces in *Indri*, *P. verreauxi*, and *P. diadema*, Demes and colleagues (1995) found that both take-offs and landings nearly always resulted in tree sway, and that for take-offs, the indriids lost contact with the initial

TABLE 6.1. Support diameters and effective jump distance in *Galago moholi*, *Tarsius bancanus* and *Galago crassicaudatus* (data from Crompton et al., 1993).

	Galago moholi[a]	*Tarsius bancanus*[b]	*Otolemur crassicaudatus*[c]
Effective Jump Distance	Initial Support Diameter	Terminal Support Diameter	Terminal Support Diameter
0–0.200 m	4.0 cm	1.8 cm	4.2 cm
0.201t–0.400 m	4.1 cm	1.8 cm	4.1 cm
0.401t–0.800 m	4.2 cm	2.4 cm	4.1 cm
0.801t–1.600 m	4.4 cm	2.8 cm	4.1 cm
1.601t–3.200 m	5.3 cm	3.0 cm	4.3 cm
3.200 m +	6.2 cm	3.7 cm	3.1 cm

[a] Diameters for all leap categories above 0.800 m were significantly different ($P < 0.05$) from each of those below (Duncan's multiple range test); [b] diameters for all leap categories above 0.400 m were significantly different ($P < 0.05$) from each of those below (Duncan's multiple range test); [c] diameters for leap category 3.200 m + significantly different ($P < 0.05$) from each of those below (Duncan's multiple range test).

support before rebound occurred, so that energy was lost to the branch at take-off as well as landing. Crompton et al. (1993, and see Table 6.1) however found that in *G. moholi,* leaps over 0.8 m began on larger diameter supports than did shorter ones, suggesting that the risk of energy loss to the substrate might have an effect on the choice of take-off supports. This was not the case in *T. bancanus*, which, on the other hand, tended to land on substantially larger supports for leap lengths over 0.4 m than for leaps up to 0.4 m; *Otolemur*, however, favored smaller supports in leaps over 3.2 m than in all leap lengths below this distance. There is thus no conclusive evidence for a consistent pattern of avoidance of loss of energy to the substrate either on take-off or on landing. But substrate orientation also needs to be taken into consideration, as does trajectory, since it might also be the case that leaps with flatter trajectories, when taken from a horizontal or low-angled support, may exert the greater proportion of take-off force in the strongest direction of the support. Conversely, leaps with higher trajectories might be expected to exert a greater proportion of force in the strongest direction of the support when taken from high-angled supports.

Discussion

Ability to use a high take-off angle requires that the body center of gravity be positioned along, or close as possible to, a line extended at that angle to the take-off support from the propelling limb(s). Assuming, as is appropriate for prosimian primates, it will be the hindlimbs which are primarily responsible for propelling a leap, the implication is that an orthograde trunk posture needs to be adopted. High take-off angles are thus more readily attained from supports at a relatively high angle to the horizontal, although they can be performed even from horizontal supports, as a consideration of the locomotor ecology of ground-foraging genera such as *Tarsius* (and to a lesser extent *Galago moholi*, for example) makes immediately obvious.

If the finding of Crompton et al. (1993)—that the specialist leaper among their five experimental subjects used steeper trajectory leaps in leaps of all lengths, whereas the generalists used steeper trajectories in only their longest leaps—could be generalized, it would then be expected that more specialized leapers, which would be more likely to avoid flat trajectories, would also be more likely to use near-vertical supports. From a pronograde body posture, low take-off angles, and thus low trajectories, with short flight times, can more readily be adopted. Leaping from low-angled supports is more feasible, and more of the thrust may be directed along the strongest axis of the takeoff support, reducing energy loss to the branch and hence branch displacement. Both a short flight time and lack of disturbance of vegetation might be seen as advantageous in predator-avoidance. But mechanical energy costs are inevitably high, and ranges short.

Hence, use of high angled supports for take-off would be expected to be more characteristic of specialist leapers, low-angled supports characteristic of more generalized leapers. This appears generally to be the case, both in comparisons of closely related pairs such as *G. moholi* and *O. crassicaudatus* (Crompton, 1984) and in broader comparisons of the prosimians as a whole (Oxnard et al., 1989). However, comparison of the behavior of *G. moholi* between different seasons shows a greater affinity for vertical supports in a cold, dry season, but lower affinity in a warm, wet season (Crompton, 1984). This would not be expected simply from an association, in nature, of steep trajectories with near-vertical take-off supports, but flat trajectories with low-angled supports. Consideration of height of observation and support availability in the open *Acacia* woodland, which is the natural habitat of *G. moholi*, shows that as *G. moholi* are found much more often low down in the cold, dry season, they will encounter fewer low-angled supports and more high-angled supports. Leap distances are longer; this would be expected *both* from the greater separation of supports nearer ground level and from an hypothesized association of steep trajectory leaps with high-angled supports.

Field data also show that mean leap length in specialist leapers is far below the attainable maximum. In *G. moholi* and *T. bancanus*, while the longest leaps observed in the field were often in excess of 4 m (Crompton, 1980, 1983, 1984; Crompton & Andau, 1986), and while Niemitz (1979) suggests over 6 m may be attained by *T. bancanus* when pursued, Crompton (1980, 1983, 1984) found that the mean leap length was only 0.69 m for *G. moholi*, and Crompton & Andau (1986) obtained a mean of 1.12 m for *T. bancanus*.

This might suggest that under field conditions, these specialist leapers do not use the ballistically optimum take-off angle as regularly as they do in the laboratory, preferring the shorter flight duration and greater unpredictability of a relatively "flat" jump; *or* that they are using asymmetric leaps, again for unpredictability because of the potential for change in direction we have mentioned above; *or* that they are interrupting their leaps by use of air resistance (perhaps less likely in small species) *or* that they often use the ballistic trajectory to gain height by landing early in the trajectory, rather than using climbing for height gain (since it may be even more expensive than height change by leaping). It may be relevant that in field data for *T. bancanus*, *G. moholi*, and even *O. crassicaudatus*, the longest leaps tended to be associated with height gain rather than height loss (Crompton et al., 1993), suggesting that these might be such interrupted ballistic leaps.

Indeed, re-analysis of Crompton's field data shows that even unspecialized arboreal quadrupeds as *O. crassicaudatus* (about 1300 g) regularly attain distances like as *G. moholi* (185 g). Some care must be taken in discussing raw leap lengths, as calculations of the mechanical cost of a leap must take into consideration the height of initial and terminal supports (see, e.g., Crompton et al., 1993; Warren & Crompton, 1998). Further, maximum ranges recorded in the field are difficult to compare, both because *Otolemur* moves much higher (see Crompton, 1984), and can thus lose much more height, and because in unusual circumstances (such as when it is being chased) it can alter leap kinematics. For example, when being chased *Otolemur* can (no doubt at some energetic cost) take off and land hindlimb first, and will then often use vertical or near-vertical supports (Crompton, 1980): This presumably gives high trajectories and therefore increases range. Re-analysis of Crompton's field data, however, shows that means for *level* leaps are very similar (0.63 m and 0.64 m, respectively, not significantly different).

While the frequency of leaping in the folivorous specialist leapers *Avahi occidentalis* and *Lepilemur edwardsi* is similar to that in *Tarsius bancanus*, their mean leap length at the study site of Ampijoroa is greater than in the latter species: 1.5 m and 1.23 m, respectively. (For the lemurs, a t-test on a 50% random sample for mechanically effective ranges gave a two-tailed, equal-variance probability of < 0.001 for overall means of 1.38 m (*Lepilemur)* and 1.56 m (*Avahi*), (Warren & Crompton, 1998)). However, this is still considerably less than the mean inter-trunk distance (2.55 m, $N = 613$, SE 0.09) at this site, and much less than the maximum leap distance that both species were observed to attain (7 m). The ability of each of these species to cross the wide gap between tree trunks is not often used. Thus, the importance of the ability to leap long distances may rather be that an ability to perform occasional very long leaps is an effective means of avoiding predation in open cover. We must however ask *why* this ability is not often used. The contribution of the mechanical costs of locomotion to the total energy budget was estimated by Charles-Dominique and Hladik (1971) and Hladik and Charles-Dominique (1974) for *Lepilemur mustelinus leucopus* in Didiereaceae bush. Their estimates suggest that the caloric value of dietary intake was insufficient to sustain total energetic costs, and they proposed caecotrophy as a possible means whereby the deficit might be made up. The predicted deficit existed, they argued, notwithstanding the fact that locomotor costs contributed only 10% to the total energy expenditure. Their conclusions have, however, subsequently been challenged by Russell (1977).

It is difficult to reliably predict the metabolic costs of locomotion, unless a forward-dynamic musculoskeletal model is used to estimate the metabolic cost of muscle contraction, as we did recently for walking in *Australopithecus afarensis* (Sellers et al., 2005). Nevertheless a case can be made that the costs of leaping locomotion in species with unusual dietary habits may be such as to bring the total budget close to tolerable limits. This particularly applies to small-bodied species where thermoregulation is highly expensive (Karasov, 1981; Schmidt-Neilsen, 1990). The most rigorous estimate of the contribution of locomotion to total metabolic costs of wild animals (the field metabolic rate, FMR) is that of Kenagy and Hoyt (1990) for golden-mantled ground squirrels. Their estimate of 15% contrasts with the figure of 2% calculated by Nagy and Milton (1979) for mantled howler monkeys. Warren & Crompton (1998) used their field data to estimate the contribution of locomotion to total energy costs for five nocturnal prosimians: four specialist leapers (*L. edwardsi, A. occidentalis, T. bancanus, G. moholi*) and one generalist (*O. crassicaudatus*) and found that *Avahi* had the highest contribution at 3%. But they noted that the contribution of locomotion to FMR is very sensitive to daily movement distances (DMD) (Goszczynski, 1986; cf.) daily path length), which are (notoriously) underestimated in observational studies of ranging behavior. Elastic energy savings through ricochetal leaping are one (untested) means whereby *Avahi* may be able to tolerate its rather high locomotor costs. Warren & Crompton (1998) suggested that *T. bancanus* might also be close to its energetic limits, on the basis of Niemitz's (1985a) and Jablonski and Crompton's (1994) data on dietary intake, and Crompton's (1989) data on DMD in *T. bancanus*. Thus, for a leaping specialist with a long DMD (such as *T. bancanus*); or a particularly low metabolic rate (such as *L. ruficaudatus* (Schmid & Ganzhorn, 1996), the energetic costs of leaping may indeed be critical, and particularly expensive leaps may need to be avoided except in life-threatening situations (of which predation must surely be the most common).

Thus, rather than concluding—as one might from the marked difference between mean and maximum leaps of *Galago*, *Otolemur*, and *Tarsius* (see above)—that specialist leaping species are "over-specified" in terms of their morphological adaptation to leaping, consideration from a predator-avoidance perspective suggests that the ability to perform long leaps may be selected for primarily by the risk of predation attempts: such attempts are likely to be far less rare than successful predation.

Clearly, if a threatened bushbaby or tarsier performs a leap some four times longer than its mean leap length, this capability would likely confuse a predator familiar with their quotidian performance. However rare, such a capability would be strongly selected for wherever predation pressure was substantial, as the effects of a successful predation on reproductive fitness are uniquely drastic (Lima & Dill, 1990).

Günther et al. (1991) suggest that specialist leapers such as *G. moholi* also tend to use asymmetrical leaping quite often, where one hindlimb applies more force than does the other, so to effect changes in direction; whereas, these authors argue, less specialized leapers do not. Asymmetrical leaping is commonly seen in other vertebrates such as frogs, where leaping is regarded as primarily a predator avoidance strategy since it reduces the predictability of leaping direction (Gans & Parsons, 1966). In invertebrates such as locusts and grasshoppers, escape leaps seem to have a completely random direction. Thus, leaping specialization in prosimians may not be so much an adaptation to maximize the leap length that can be obtained, as an adaptation to maximize the leap length that can be obtained using the force from one hindlimb. In other words, it may be that specialist leapers are adapted to perform well in *asymmetric* leaping rather than *symmetric* leaping. This argument would, however, also be consistent with their specialization serving the ends of unpredictability (and so predator avoidance, and where relevant, predation) rather than locomotor efficiency. It could also be the case in species where energetic budgets are so finely balanced (perhaps including *T. bancanus*, *A. occidentalis*, and *L. edwardsi*) that a high degree of locomotor efficiency is also selected for.

Finally, extra leaping performance may allow leaps to be performed at energetically suboptimal trajectories. This increases the energetic cost of the leap but can reduce the flight time and increase the horizontal speed, or allow reduction in the predictability of the trajectory—all potentially valuable methods of avoiding predators. However, since use of flat trajectories is actually rather commoner in unspecialized rather than specialized leapers, this factor is not likely to be important.

Goodman et al. (1993) provide an excellent review of the anecdotal data we have on predation on lemurs. While snakes appear to be less frequent predators, the fossa (*Cryptoprocta ferox*), and to a lesser extent other viverrids, such as *Galidia elegans*, frequently prey on diurnal and nocturnal lemurs, large and small alike. Owls, such as the barn owl (*Tyto alba*) and the Madagascar long-eared owl (*Asio madagascariensis*) are primarily predators of small-bodied, nocturnal genera such as *Microcebus,* while large raptors, such as the Madagascar harrier hawk (*Polyboroides radiatus*) and the Madagascar buzzard (*Buteo brachypterus*) prey on large-bodied, diurnal genera, including *Propithecus* and *Indri*. Defensive movements made by adult *Indri* at Mantadia when *Polyboroides* is in sight suggest the latter is a predator on young *Indri*. Both *Polyboroides* and *Buteo* elicit alarm calls from *Hapalemur griseus* at Mantadia, are often heard circling *Hapalemur* home ranges, and are likely major predators (Mary Blanchard pers. comm. and authors' pers. obs.). These data imply, and the "short-winged" nomen of the Madagascar buzzard reminds us, that we need to consider the locomotor capabilities of predator species as well as those of their prey. Short-winged birds, such as most owls, are generally more capable of rapid changes of direction (see, e.g., Norberg, 1985), whereas long-winged species may only be capable of taking lemurs from the very top of the canopy.

Cryptoprocta, the fossa, is a large-bodied but short-legged carnivore, den-living but competent arboreally and capable of leaping (see, e.g., Wright et al., 1997; Hawkins, 1998; Dollar, 1999; Dollar et al., this volume; Patel, 2005). The fossa's powerful forelimbs, clawed digits, and short, flexed limbs permit pursuit by climbing on large to medium size tree trunks and branches. Because it is a large predator, we would expect and indeed find that *Cryptoprocta*, in preying on small lemurs, will concentrate on nocturnal species that use nests or tree-hollows for sleeping (and may sleep in groups), rather than risk failure in an active chase. A rare film sequence (an edited version can be seen in BBC Wildlife, *Life of Mammals*) of

Cryptoprocta in pursuit of *Propithecus* show that while the fossa is quite capable of leaps of one to two meters (level) from, and to, vertical supports, it is less agile than a sifaka on smaller, low-angled branches, where body weight deforms the support, but where the fossa's lack of grasping appendages renders it unstable. In the case of the BBC film, however, it appears to have been primarily the sifakas' ability to make repeated leaps with frequent and marked changes of direction that leads to their escape.

Predation by raptors on large lemurs almost inevitably occurs most often at canopy level or in open ground, as long wings and a soaring habit do not permit ready flight in woodland, where frequent changes of direction are required. This may suggest one reason why indris tend to travel from tree to tree just below canopy level, despite the long leaps that are required. *Indri* appear to avoid having to come to the ground (Mary Blanchard, pers. comm.), where they are at a disadvantage with respect to *Cryptoprocta*. Bipedal hopping by *Propithecus* may, however, permit this genus more extensive use of the ground and lower forest levels by permitting confusingly sudden changes in direction when pursued by these predominantly quadrupedal predators.

Predation on galagos was discussed briefly by Bearder (1987) who estimated that 15% of *G. moholi* populations are harvested annually by predators, primarily owls but also, during the day, hawks. During the day, *G. moholi* and its sympatric relative *O. crassicaudatus* are relatively protected by the long thorns of the *Acacia* trees (the gums of which contribute substantially to their diet). At night, *Otolemur* exhibit alarm in the presence of genets (*Genetta tigrina*). The genet is an agile, arboreal species like itself. On the other hand, even young *Otolemur* will approach and touch monitor lizards of considerable (about one meter) size if they are found on a branch (author Crompton pers. obs.). Rapidity in movement seems to be a prerequisite for nocturnal predators on galagos. However, there is no doubt that owls are agile enough to take *Galago* in mid-leap: it happens commonly enough to have been captured on film (BBC Wildlife, *Mara Nights*). In contrast, instances of predation on tarsiers are relatively rare in the literature. MacKinnon and MacKinnon (1980) remark on a lack of any alarm response by tarsiers to the presence of potential predators. On the other hand, Gursky (2001) reported a successful predation on *Tarsius spectrum* by a python and (2005) noted frequent alarm calling and mobbing in response to potential predators, and Susmann (1999) reported that Shekelle has observed a predation event on *T. syrichta* by a monitor lizard. But the Sulawesi and Phillippine forest habitats are relatively open compared to lowland evergreen rainforest, the habitat of the largest species, *T. bancanus*.

Niemitz (1979) working on *T. bancanus* in a forest enclosure at Semongok, Sarawak, observed that this species lacks any obvious alarm response to potential predators introduced into the enclosure. Similarly, Crompton, working at Sepilok in Sabah, did not observe predation or any suggestion of an alarm response during the active period in many hours of close-contact following of free-ranging *T. bancanus*. This species usually forages within the first two meters above the ground. In the normal primary rainforest habitat of this species, little moon- or starlight (and relatively little sunlight) reaches this level. Thus, at night *T. bancanus* must be very difficult for any predator to locate, since its background will always be relatively dark, and lacking a tapetum, light that does reach it will not be reflected back from its eyes. (It does not seem likely that absence of a tapetum is related to a cryptic "strategy." The tarsier's lack of a tapetum is of course amply compensated by eye size and a likely consequence of secondary adoption of nocturnality by its branch of the common haplorhine lineage (Crompton, 1989). Nocturnality serves niche differentiation more directly than it does crypsis). Crompton found *T. bancanus*' habitual response to (human) pursuit to be immediate flight by a rapid series of upward leaps to a height of up to 12 m. Similarly, vine and thorn tangles at 3–4 above ground (well above the normal height of activity) in dense tree fall zones were identified as the commonest diurnal sleeping site. This suggests that diurnal terrestrial predators may be more of a problem for this species.

Conclusions

As we have seen, it has often been proposed that the single greatest advantage conferred by leaping locomotion is the ability to make sudden and unpredictable changes in direction: in anurans (Gans & Parsons, 1966), fleas (Bennet-Clark & Lucey, 1967), and locusts (Bennet-Clark, 1975, 1977). Amongst mammals, a very clear case for this argument is that made for the hopping of pocket mice by Bartholomew and Cary (1954), which rarely use their hopping as a means of travel, preferring to use quadrupedalism unless threatened. It is therefore most economical to conclude that while no single selective pressure is likely to be responsible for the widespread adoption of leaping locomotion by prosimian primates, the balance of the weight of evidence suggests that as in many non-primate leapers, prosimian leaping has been adopted primarily as a predator-avoidance device. As one of the most striking characteristics of prosimians, this in turn suggests that—outside of infancy, dormancy, or the inactive part of the diel cycle, and with the possible exception of the lorises—crypsis, as a predator avoidance strategy, is no more typical of what Bearder (1987) aptly terms "solitary foragers," the small-bodied, nocturnal forms, than it is of the large-bodied, diurnal, social foragers.

Future Directions for Research

In his recent but already classic text, Alexander (2003) observes that a major need in locomotor biology is for studies of the mechanics of arboreal locomotion that take account of the flexibility and uneven spacing of branches. We need more locomotor studies designed to collect biomechanically relevant data, rather than just raw locomotor counts, and to allow integrated analysis of leap length (raw and effective), and initial and terminal support characteristics. This study suggests that we need to understand the decisions made by animals crossing gaps between such supports in terms of the costs and risks (both biomechanical and ecological) that each choice incurs. Among these risks predation must surely be the most adaptively challenging.

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Appendix 1. Leaping Mechanics

A leaping prosimian can be considered a projectile and the mechanics of projectiles are well understood. The basic equations can be found in most mathematics textbooks and a worked derivation can be found in, for example, Norton (1987).

In the general case (as illustrated in Figure 4) an animal leaps a distance R (measured in meters) at an angle α to the horizontal (α is positive for an upward leap and negative for a downward leap). This angle will be referred to as the *slope* of the leap. The actual horizontal distance is R cos α and the vertical height change is R sin α. The animal achieves this leap by taking off at a velocity of **U** m/s at an angle φ to the horizontal. g is acceleration due to gravity: 9.81 m/s. The flight time for a given leap can be calculated using equation (6.1) and examples are shown in Figure 6.2

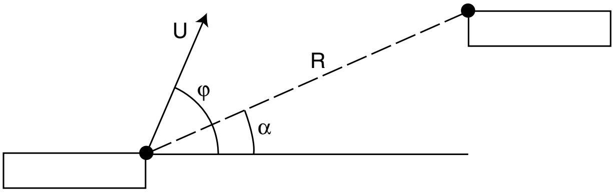

FIGURE 4. Diagram illustrating an animal leaping between supports at different heights from the ground

$$t = -\frac{2U\,\mathrm{Sec}[\alpha]\mathrm{Sin}[\alpha - \phi]}{g} \tag{6.1}$$

Similarly the range for a given leap can be calculated using equation (6.2) and examples are shown in Figure 6.3. For any given combination of support heights (slope) there is a take-off angle that will maximize travel distance (and hence minimize energetic cost of travel). This can be calculated directly using equation (6.3). The range for this maximally efficient leap can be calculated from equation (6.4).

$$R = -\frac{2U^2\mathrm{Cos}[\phi]\mathrm{Sec}[\phi]^2\mathrm{Sin}[\alpha - \phi]}{g} \tag{6.2}$$

$$\phi_{\mathrm{eff}} = \frac{90 + \alpha}{2} \tag{6.3}$$

$$R_{\mathrm{max}} = -\frac{U^2\mathrm{Sec}[\alpha]^2(-1 + \mathrm{Sin}[\alpha])}{g} \tag{6.4}$$

The mechanical energy cost of a general leap can be calculated using equation (6.5) and examples are shown in Figure 6.1. Variable m is mass of the animal in kg.

$$KE = -\frac{1}{4}gm\,R\,\mathrm{Cos}[\alpha]^2\mathrm{Csc}[\alpha - \phi]\mathrm{Sec}[\phi] \tag{6.5}$$