

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

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ABSTRACT

Prosimian primates are unique among vertebrates for their leaping abilities, some small species being able to leap over four metres level, or attain height gain of over two metres; some larger species 8-10 metres level. Field and laboratory data suggest however that these capabilities are rarely recruited, and that most level leaps are little more than a quarter of these distances. In the laboratory, the energetically optimal take-off angles are rarely used by most prosimians, and at least some unspecialized forms seem to be able to match the leaping capabilities of the most specialized leapers. Theoretical considerations and field data suggest that what long leaps offer in particular is unpredictability. While no single factor, acting alone, is likely to account for the widespread adoption and adaptive diversity of the leaping specialization, we suggest that as in other animals, leaping was adopted originally and primarily as a predator-avoidance mechanism, enabling prosimians to make sudden, unexpected and repeated changes of direction under threat of predation.

KEY WORDS

Avahi, Biomechanics; ecology; *Galago*; leaping; *Lepilemur*, locomotion, prosimian, *Otolemur*, *Tarsius*

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 favour of adaptations which 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, eg. Terborgh and 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’ is often regarded as facilitating an alternative predator avoidance strategy, crypsis (eg. Clutton-Brock and 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 which 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 four metres and height gains of over two metres may be performed. 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 tail-less, with subequal 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 behaviour has been described as ‘stealthy’ (Walker, 1969), slow movement, it was claimed, being 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 movement predatory movement is served by leaping. Although an apposite characterization of the behaviour 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 and Andau 1986; Oxnard et al. 1989; Jablonski and 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 (ie. 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, eg. 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 ms^{-1} ; 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: theory, and data from the laboratory and field

1) Leaping style and leaping mechanism

Three categories of leaping ‘style’ (see eg. Oxnard et al., 1989) have been defined: static leaping where the animal pauses before making a leap; running leaping where the animal makes a transition from a run to a leap; and ricochetleaping where 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 eg. Alexander, 2003) used to generate the power required for leaping: squat leaping where muscle contraction alone is the motive force; countermovement leaping where a previous movement is used to store elastic energy that is released during takeoff; catapult leaping where a locking mechanism is used to allow muscles slowly to bring about maximum tension which can then be quickly released during takeoff; and vaulting leaping, where a rigid strut is used to alter the direction of movement of the centre of mass. All these mechanisms are potentially applicable to all the leap styles (with the probable exception of vaulting combined with ricochetleaping), but it is most likely that the squat, catapult and countermovement mechanisms are all used to perform static leaps. Countermovements are also involved in ricochetleaping. 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), that is, 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, and which allow them to apply smaller forces over a longer take-off period, scaling effects also suggest that muscle physiological cross sectional area will be larger compared to body mass in small mammals (see eg. Demes and Günther, 1989), so that even though the reduced takeoff 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 (and see also Bennet-Clark [1977]), which implies the existence of some means of power amplification. A dynamic analysis by Aerts (1998) led him to suggest that the required power amplification can be obtained by a sequential recruitment of countermovement, catapult and squat ‘with compliant tendons’ (Alexander, 1995) mechanisms.

2) 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 which are leaps, or the contribution to each kilometre of travel which is made up by leaping. Although armswinging is used to extend a series of leaps by sifakas (RHC 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 centre 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 their small body size, the tail-flick presumably must act by changing the rotational inertia of the body, not by means of air resistance (Peters and 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 lack 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 which 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 takeoff were larger still.

3) 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 and Anderson, 1988). Except for ‘ricochetal’ leaping, where leaps follow immediately upon each other, at a stable resonant frequency, there is little or no possibility for conserving energy between one leap and the next. Energy savings in ricochetleaping 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: eg. 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.)

4) 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 behaviours which result in large forces are likely to influence musculoskeletal morphology (Alexander, 1981). As we have seen, the scale of forces required to be exerted in takeoff varies with body size, so that Demes and colleagues (1999) give values of hindlimb takeoff force of thirteen times body mass in *G. moholi*, but nine times body mass in *Propithecus verreauxi*. Their more striking contrast was however with quadrupeds of equivalent size, where forces are 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.

5) Leaping and transport speed

In contrast to popular expectation, leaping is not a particularly fast method of travel. Again, leaping is also not a particularly fast means of getting around. Günther et

al. (1991) recorded maximum velocities at take-off of 5.1 ms^{-1} for *G. moholi* leaping from a forceplate, and noted that this compares unfavourably to velocities of 15 ms^{-1} 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 ms^{-1} required by leapers to attain a height of one metre, irrespective of size (according to Bennet-Clark, 1977). As *Galago moholi* (according to Hall-Craggs [1964, 1965]) can gain 2.25 m in a leap, 5.1 ms^{-1} must be an underestimate of actual maxima (although doubling the vertical takeoff velocity would quadruple the height gain, [Bennet-Clark, 1977]). However, under natural conditions, Crompton recorded only a single record of two metres' estimated height gain and only 39 of over one metre estimated height gain, in 2786 leaps by *G. moholi*. For *Tarsius bancanus*, he recorded a maximum of 1.5 metres' estimated height gain, and only eight records of leaps over a metre height gain (of a total 1425 observed leaps). These field data tend to suggest that a takeoff velocity of 5.1 ms^{-1} (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 ms^{-1} (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 takeoff, varies with takeoff 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 1-3 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.

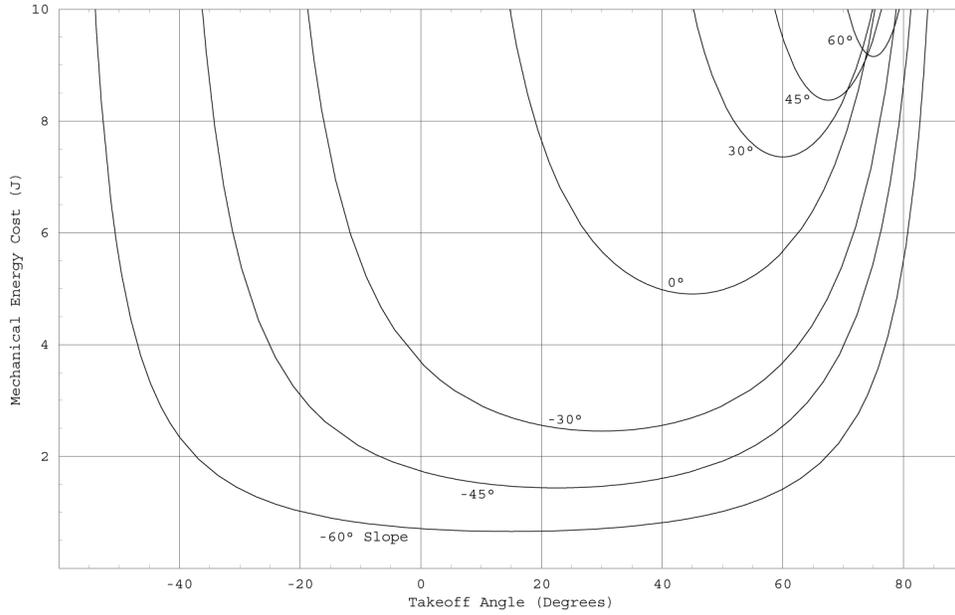


Fig. 1.

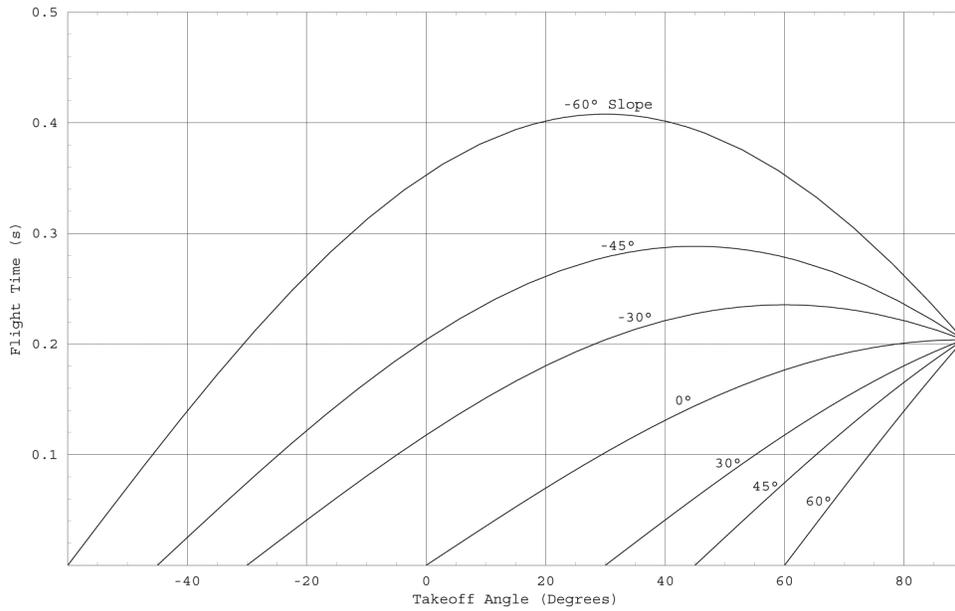


Fig. 2

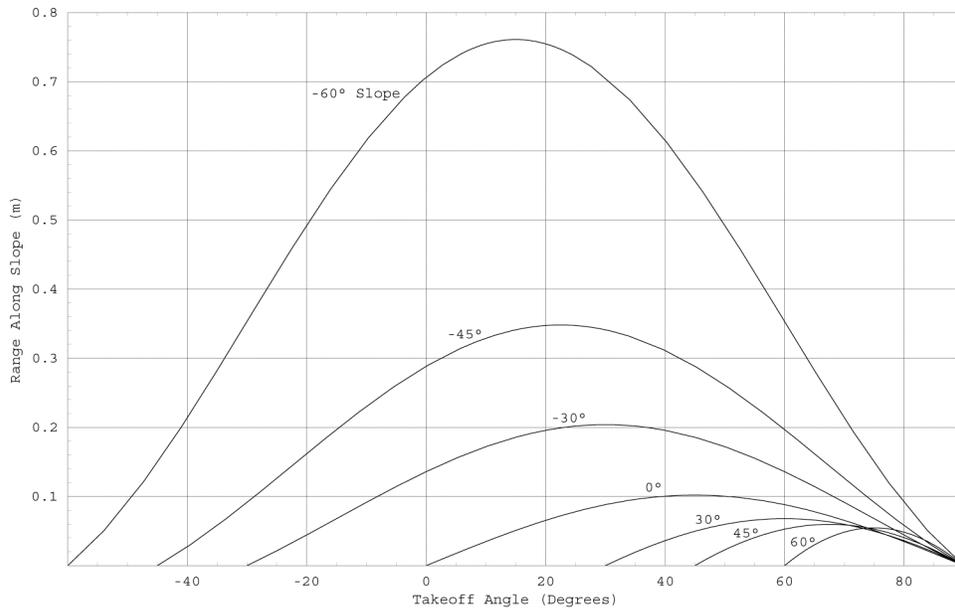


Fig. 3

Figure 1 shows the mechanical energy cost of a leap for a set of takeoff angles, given the relative height of the initial and terminal support ('slope') for a 1 kg animal leaping 1 m. Figure 2 shows the flight time for a range of takeoff angles and differing relative heights of initial and terminal supports ('slope'), again for a 1 m s^{-1} takeoff velocity (the range for any combination of these values are given for equivalent values in Figure 3). Flight times for different takeoff velocities are simple multiples so the flight time for a speed of 2 m/s would be twice the value given, for 4 m/s it is 4 times the value, etc.). Figure 3 shows the range of a leap for a set of takeoff angles and 'slopes' for a 1 m s^{-1} takeoff velocity. The range distance shown is the length of a line drawn from start to end point, the horizontal distance can be obtained by multiplying by the cosine of the 'slope' 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 takeoff angle that will maximise travel distance (or equally minimise the energetic cost of travel). For level leaps, at a takeoff angle of 45° , distance covered for a given takeoff force is maximized, but such a leap is relatively slow. By contrast, a low, 20° takeoff angle gives lowest costs for a 60° descent while a takeoff angle around 75° is required for maximum efficiency in a 60° ascent. Flatter trajectories cover less distance for the same takeoff force, but less time is spent in the air. Very low takeoff angles, while minimising flight time are always energetically expensive. While in general, short flight times require low takeoff angles, for downwards leaps the longest flight times occur with moderate takeoff angles. Leaping upwards, however, is clearly much more expensive than leaping downwards.

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 takeoff 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 takeoff and landing forces than less specialized leapers such as *G. garnetti*. Takeoff force did not increase with distance (within the limited range of leap distances they could examine). In a study of leaping forces in *Indri*, *Propithecus verreauxi* and *P. diadema*, Demes and colleagues (1995) found that both takeoffs and landings nearly always resulted in tree sway, and that for takeoffs, the indriids lost contact with the initial support before

rebound occurred, so that energy was lost to the branch at takeoff as well as landing. Crompton et al. (1993, and see Table 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

Table 1 about here

energy loss to the substrate might have an effect on the choice of takeoff 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 favouring 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 takeoff 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 taking off from a horizontal or low-angled support, may exert a greater proportion of takeoff 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 taking off from high-angled supports.

DISCUSSION

An ability to use a high takeoff angle requires that the body centre of gravity is positioned along, or close as possible to, a line extended at that angle to the takeoff

support from the propelling limb(s). Assuming, as is appropriate for prosimian primates, that it will be the hindlimb(s) which are primarily responsible for propelling the leap, this implies that an orthograde trunk posture will need to be adopted. High takeoff 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 steep 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 takeoff 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 take-off 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 takeoff 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 *Galago moholi* and *Otolemur crassicaudatus* (Crompton, 1984) and in broader comparisons of the prosimians as a whole (Oxnard et al., 1989). However, comparison of

the behavior of *Galago 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 takeoff 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 maximum that can be attained. In *G. moholi* and *T. bancanus*, while the longest leaps observed in the field are often in excess of 4 m, (Crompton, 1980, 1983, 1984; Crompton and 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 and 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 takeoff 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 unspecialised arboreal quadrupeds as *Otolemur crassicaudatus* (about 1300 g) regularly attain such distances as do *G. moholi* (185 g). Some care must be taken in discussing raw leap lengths, as the mechanical cost of a leap must take into consideration the height of initial and terminal supports (see eg. Crompton et al. 1993; Warren and 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 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 .000 for overall means of 1.38 [*Lepilemur*] and 1.56 m [*Avahi*], Warren and 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 which 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 suggested 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 forwards-dynamic musculoskeletal model is used to estimate the metabolic cost of muscle contraction, as we have done 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 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 for Nagy and Milton (1979) for mantled howler monkeys. Warren and Crompton (1998) used their field data to estimate the contribution of locomotion to total energy costs for five nocturnal prosimians: four specialist leapers (*Lepilemur edwardsi*, *Avahi occidentalis*, *Tarsius bancanus*, *Galago moholi*) and one generalist, (*Otolemur 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, Goszczyński, 1986 cf. daily path length)), which are (notoriously) underestimated in observational studies of ranging behaviour. Elastic energy savings through ricochetleaping are one (untested) means whereby *Avahi* may be able to tolerate its rather high locomotor costs. Warren and Crompton (1998) suggested that *Tarsius bancanus* may 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 *Tarsius bancanus*. Thus, for a leaping specialist with a long DMD: (such as *Tarsius bancanus*); or a particularly low metabolic rate: (such as *L. ruficaudatus* [Schmid and 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, which 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 their mean leap length, this capability would be likely to 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 and 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 that changes in direction may be effected, whereas, they 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 and Parsons, 1966). In invertebrates such as seen in locusts and grasshoppers escape leaps seem to have 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 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 not *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 finely balanced (perhaps including *Tarsius bancanus*, *Avahi*

occidentalis and *Lepilemur edwardsi*) that a high degree of locomotor efficiency is also selected for.

Finally, extra leaping performance may be used to allow leaps to be performed at energetically suboptimal trajectories. This increases the energetic cost of the leap but can reduce the flight time and increases the horizontal speed, or allow reduction in the predictability of the trajectory - all potentially valuable for avoiding predators. But 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 on 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 suggests it 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 a major predator. (Mary Blanchard pers. comm. and authors' personal observations.) 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 eg. 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 viverrid, den-living but competent arboreally and capable of leaping (see eg. 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. As a large predator, we would expect and indeed find that predation by *Cryptoprocta* on small lemurs concentrates on nocturnal species which use nests or tree-hollows for sleeping (and may sleep in groups), rather than risking 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 metres (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 sequence, however it appears to have been primarily the sifakas' ability to make repeated leaps with frequent and marked changes of direction which lead 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 which 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* and other viverrids. 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 has been discussed briefly by Bearder (1987) who estimates 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 *Otolemur 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*, which is an agile arboreal species like itself. On the other hand, even young *Otolemur* will approach and touch monitor lizards of considerable (about one metre) size if they are found on a branch (RHC 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) reports that Shekelle has observed a predation event on *T. syrichta* by a monitor lizard. But the Sulawesi and Phillipines 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 *Tarsius bancanus*. This species usually forages within the first two metres above the ground. In the normal primary rainforest habitat of this species, little moon- or star-light (and relatively little sunlight) reaches this level. Thus at night, *Tarsius bancanus* must be very difficult for any predator to locate, since its background will always be relatively dark: and lacking a tapetum, light which 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 [see eg. Crompton, 1989] Nocturnality serves niche differentiation more directly than it does crypsis.) Crompton found *Tarsius bancanus*' habitual response to (human) pursuit to be immediate flight by a rapid series of upwards leaps to a height of up to 12 metres. Similarly vine and thorn tangles at three to four metres above ground (well above the normal height of activity) in dense treefall zones were identified as the commonest diurnal sleeping site. This suggests that diurnal terrestrial predators may be more of a problem for this species.

CONCLUSION

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 and Parsons, 1966); fleas (Bennet-Clark and Lucey, 1967) and locusts (Bennet-Clark, [1975] and see Bennet-Clark [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 which take account of the flexibility and uneven spacing of branches. We need more locomotor studies which are designed to collect biomechanically-relevant data, rather than just raw locomotor counts, and 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 on how to cross gaps between such supports in terms of the costs and risks (both biomechanical and ecological) 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 as a projectile and the mechanics of projectiles are well understood. The basic equations can be found in most mathematics text books and a worked derivation can be found in, for example, Norton (1987).

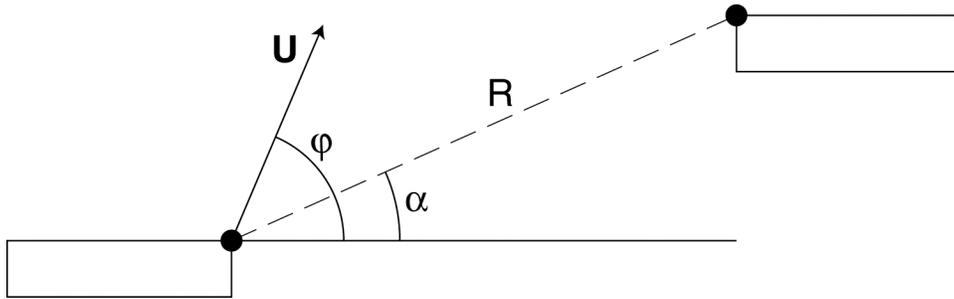


Figure 4. A diagram illustrating an animal leaping between supports at different heights from the ground.

In the general case (as illustrated in Figure 4) an animal leaps a distance R (measured in metres) 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 $R \cos \alpha$ and the vertical height change is $R \sin \alpha$. The animal achieves this leap by taking off at a velocity of $U \text{ m s}^{-1}$ at an angle φ to the horizontal. g is the acceleration due to gravity: 9.81 m s^{-1} . The flight time for a given leap can be calculated using equation 1 and examples are shown in Figure 2.

eq1.

$$t = -\frac{2 U \operatorname{Sec}[\alpha] \operatorname{Sin}[\alpha - \phi]}{g}$$

Similarly the range for a given leap can be calculated using equation 2 and examples are shown in Figure 3. For any given combination of support heights (slope) there is a takeoff angle that will maximise travel distance (and hence minimise energetic cost of travel). This can be calculated directly using equation 3. The range for this maximally efficient leap can be calculated from equation 4.

eq2.

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

eq3.

$$\phi_{\text{eff}} = \frac{90 + \alpha}{2}$$

eq4.

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

The mechanical energy cost of a general leap can be calculated using equation 5 and examples are shown in Figure 1. m is the mass of the animal in kg.

eq5.

$$KE = -\frac{1}{4} g m R \cos[\alpha]^2 \csc[\alpha - \phi] \sec[\phi]$$

Legends for Figures

Figure 1 Mechanical energy cost of a leap for a set of takeoff angles and initial and terminal supports (slopes) for a 1 kg animal leaping 1 m.

Figure 2. Flight time for a set of takeoff angles and relative heights of initial and terminal supports (slopes) for a 1 m s^{-1} takeoff velocity.

Figure 3. Range of a leap for a set of takeoff angles and relative height of initial and terminal supports (slopes) for a 1 m s^{-1} takeoff velocity. The range is measured along the slope.

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

(Fig 1 = Energy.eps; Fig 2 = Flight Time.eps; Fig. 3 = Range.eps; Fig 4 = Diagram.eps)

Table 1 Support diameters and effective jump distance in *Galago moholi*, *Tarsius bancanus* and *Galago crassicaudatus*. (Data from Crompton et al. [1993])

Galago moholi (initial supports)

0-0.200 m	0.201-0.400 m	0.401-0.800 m	0.801-1.600 m	0.601-3.200 m	3.200 m +
4.0 cm	4.1 cm	4.2 cm	4.4 cm	5.3 cm	6.2 cm

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)

Tarsius bancanus (terminal supports)

0-0.200 m	0.201-0.400 m	0.401-0.800 m	0.801-1.600 m	0.601-3.200 m	3.200 m +
1.8 cm	1.8 cm	2.4 cm	2.8 cm	3.0 cm	3.7 cm

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)

Otolemur crassicaudatus (terminal supports)

0-0.200 m	0.201-0.400 m	0.401-0.800 m	0.801-1.600 m	0.601-3.200 m	3.200 m +
4.2 cm	4.1 cm	4.1 cm	4.1 cm	4.3 cm	3.1 cm

Diameter for leap category 3.200 m + significantly different ($P < 0.05$) from each of those below (Duncan's multiple range test)