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Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates

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SUMMARY

We tend to assume that natural selection will bring about 'optimal' configurations in morphology and behaviour. Jumping locomotion involves large forces and energy costs which, in this non-cyclic activity, are generated anew with each jump. Jumping appears to be, therefore, a major target for optimization. It has been a standard assumption that jumpers will tend to adopt ballistic paths which will minimize the energy costs involved in jumping, and will act to minimize the loads applied to the body. Experimental studies, using kinematic analysis of digitized video recordings of the jump in five prosimian primates, with a 25-fold range in body mass, show that most do not adopt energy-efficient paths until the length of the jump is close to the maximum they can attain. Statistical analysis of quantified field observations suggests that, of three primate jumpers, only the largest, most unspecialized appears to take the forces applied to the musculoskeletal system into consideration when selecting supports used in locomotion. 'Ecological' factors, such as time pressure and habitat support density, may thus be the prime consideration for many species in determining the manner in which they jump.

1. INTRODUCTION

The locomotor system – the musculoskeletal system of the limbs and back which acts to maintain or alter the position of the body with respect to the external environment – has long been a chosen laboratory for studies of adaptation. It seems highly responsive to changes in the functional demands of the environment. According to Wolff's law, bone is remodelled according to strain distributions occurring under functional loads, and remodelling imposes metabolic energy costs (see, for example, Kummer 1972). All work done by muscles, whether to produce movement or resist external forces, imposes further costs (Alexander 1968, 1988). We might thus expect selection to favour habitual behaviours which minimize the metabolic energy costs of locomotion and the loads which the skeleton must sustain, and for evolution to configure morphology to the same effect.

The mechanics of jumping locomotion (reviewed in Bennet-Clark 1977; Peters & Preuschoft 1984; Emerson 1985) are ruled by simple ballistic laws, and hence are relatively easy to analyse. Jumping involves forces which are relatively large compared with those occurring in other activities and, because it is a non-cyclical activity, there is no possibility for conservation of kinetic and potential energy. The same lack of cyclicity means that its total (physiological) energy costs are difficult to measure. The few data that exist (Taylor *et al.* 1982; Walton & Anderson 1988) confirm that jumping is an expensive mode of locomotion. A partial measure may be gained by calculating its kinetic energy costs. E_{KE} , the external kinetic energy

cost of a jump (Fedak *et al.* 1982), may be calculated for any takeoff angle θ , by using the following equation, derived from standard ballistic equations (Norton 1982; see Bennet-Clark 1977; Emerson 1985):

$$E_{KE} = mgr/2 \sin 2\theta, \quad (1)$$

where m is the animal's mass, g is the gravity constant, and r is the horizontal distance leapt.

It has long been understood (see, for example, Alexander 1968) that, because jumping is a ballistic activity, the longest (or the most energy-efficient) level jumps can be made when the body is accelerated at a takeoff angle of 45° (see figure 1, where values of E_{KE} are plotted for various takeoff angles). Laboratory studies on the small prosimian *Galago moholi* (Treff 1970) found that this species does follow the prediction for energy optimization, taking off at 45° . Studies of leaping have concentrated on the mechanisms available for animals to generate the required forces, and in particular the problems encountered by small leapers, which have limited limb length and hence a limited period in which forces can be generated and applied to the support. Bennet-Clark (1975) showed that in locusts there is inadequate time for muscles to generate the forces required to make leaps of the distances observed, and that a mechanism exists allowing the force of muscle contractions to be stored as elastic strain energy, and released during take off.

Bennet-Clark (1977) suggested that this may also be the case in *G. moholi*, but no mechanism has yet been shown to exist. As this species covers 55 m of every 1000 m travelled by bipedal hopping (Crompton 1980, 1984), it may be relevant that studies of the mechanics

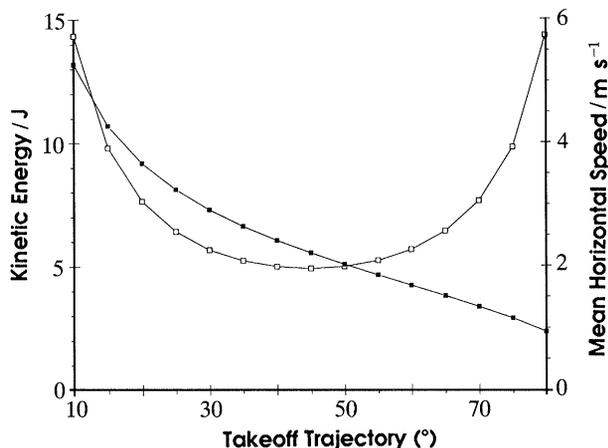


Figure 1. Theoretical kinetic energy cost (for a 1 kg subject) (open squares) and mean horizontal speed of jumps (filled squares), at different takeoff angles.

(Biewener *et al.* 1981) and energy costs (Thompson *et al.* 1980) of hopping in small mammals suggest that there is little possibility for elastic storage in such species, and show that hopping is an expensive form of locomotion which may be selected for as a means of predator avoidance (see also Gans & Parsons 1966). External energy stores have also been proposed. Alexander (1991), however, cautions that for primates, living in an arboreal milieu, the compliance of the supports on which locomotion occurs is more likely to result in loss than gain of energy. In terms of the energy costs of locomotion, it will be disadvantageous for an animal to impart energy to the branch at takeoff, unless the natural frequency of the branch is such that the animal can recover this energy by gaining thrust from elastic recoil. However, the corollary of his argument is that energy loss to the branch will be advantageous on landing. Then, to the extent that the branch is not compliant, and the potential and kinetic energy of the jump are not converted to strain energy imparted to the branch, the energy of the jump will have to be dissipated by the musculoskeletal system.

In this paper, we re-examine the proposition that primate jumpers should be expected to take off in such a way as to minimize energy expenditure, but land in such a way as to minimize skeletal loads by loss of energy to the environment. Our technique is to apply the same physical principles to analysis of observational field data as to controlled, laboratory experiment, thus combining Alexander's (1988) 'ecological' and 'functional' morphology. We leave for a further publication the question of scaling effects, which previous studies by Bennet-Clark (1977), Preuschoft (1989) and our own work (see, for example, Sellers 1992; Demes & Günther 1989) suggest are complex and not explicable by any single model of similarity.

2. METHOD

Our subjects are six prosimian primates, four of which jump in at least 20% of displacements, two less often (Oxnard *et al.* 1990). We have used two kinds of data: (i) quantitative field data on the relation between jump length, height change and support diameters; and (ii) kinematic studies of takeoff trajectories. For practical reasons, it has not been possible to

study all six species with each technique. *Galago crassicaudatus*, *G. moholi* and *Tarsius bancanus* were examined in field studies, but *Galago garnettii* (the sister-taxon of *G. crassicaudatus*), *G. moholi*, *Microcebus murinus*, *Mirza coquereli*, *Cheirogaleus major* and *Lemur catta* were the subjects of our kinematics. However, the overlap is certainly sufficient to allow meaningful comparisons.

The two small species *G. moholi* (3258 recorded jumps) and *T. bancanus* (1406 jumps) have a suite of behavioural and morphological characteristics, such as extreme elongation of the hindlimb, which have traditionally been regarded as 'specializations' for leaping (see Peters & Preuschoft 1984). The larger species, *G. crassicaudatus* (1249 jumps) has these characteristics to a much lesser degree. Jump length, initial and terminal support diameter and heights and orientation (because the angle of the support relative to the takeoff trajectory might also affect its effective diameter), together with a range of ancillary behavioural information, were observed in free-ranging animals in their natural habitat. The method for these quantitative observational studies is discussed in Crompton (1980, 1984) and Crompton & Andau (1986). Data on terminal supports has not previously been reported. The effects, on compliance and natural frequency, of branch length and diameter (see MacMahon & Kronauer 1976), and indeed tree species and leaf phenology, will be addressed elsewhere. Here, we include only the interacting (Crompton 1984) effects of branch height, orientation and diameter.

The appropriate distance measure to use for a study of the mechanics of jumping is not the actual recorded jump distance but the effective distance, X_e . This is the maximum possible length of a level jump with the same takeoff speed. To avoid *a priori* weighting, we assumed that takeoff angles were 45°.

X_e was calculated from an equation derivable from equation (1):

$$X_e = r \cos^2 \alpha / (1 - \sin \alpha), \quad (2)$$

where α is the angular displacement from the horizontal of the end point of the leap, and r is the horizontal distance in metres. We then compared the mean diameter and orientation of initial and terminal supports, and the amount of any height change for different values of X_e , by using Duncan's multiple range test (recommended for similar purposes in Norusis & SPSS Inc. 1988).

Secondly, to analyse species differences in takeoff trajectories under experimental conditions, we videotaped *G. moholi*, *G. garnettii*, *Microcebus murinus*, *Mirza coquereli* and *Cheirogaleus major* jumping between rigid horizontal supports, with no height difference, and separated by distances of 0.3 m, 0.5 m, 1.0 m and 1.4 m. In addition, *Lemur catta* was filmed jumping over a single distance of 2.25 m (practical considerations prevented the identical set-up being used). The data were analysed by using custom-written software which converted each video frame into a digital bitmap stored on a computer. These images were then calibrated and measured by using a mouse cursor from within the program, and the segment kinetics were calculated. Using data for segment mass distribution allowed us to calculate the instantaneous position of the overall body centre of mass for each frame, and hence the angle from the horizontal of the takeoff trajectory (method is detailed in Sellers (1992) and Sellers & Crompton (1993)).

3. RESULTS

Analysis of the field data (table 1) shows that there is no significant increase in initial support diameter with increasing jump length in *G. crassicaudatus* and *T.*

Table 1. Mean support diameters in relation to effective jump distance

<i>Galago moholi</i> (initial supports):					
0–0.200 m	0.201–0.400 m	0.401–0.800 m	0.801–1.600 m	1.601–3.200 m	3.200 m +
4.0 cm	4.1 cm	4.2 cm	4.4 cm	5.3 cm	6.2 cm
All categories above 0.800 m significantly different ($p < 0.05$) from each of those below.					
<i>Tarsius bancanus</i> (terminal supports):					
0–0.200 m	0.201–0.400 m	0.401–0.800 m	0.801–1.600 m	1.601–3.200 m	3.200 m +
1.8 cm	1.8 cm	2.4 cm	2.8 cm	3.0 cm	3.7 cm
All categories over 0.400 m significantly different ($p < 0.05$) from both of those below.					
<i>Galago crassicaudatus</i> (terminal supports):					
0–0.200 m	0.201–0.400 m	0.401–0.800 m	0.801–1.600 m	1.601–3.200 m	3.200 m +
4.2 cm	4.1 cm	4.1 cm	4.1 cm	4.3 cm	3.111 cm
Over 3.200 m category significantly different ($p < 0.05$) from all those below.					

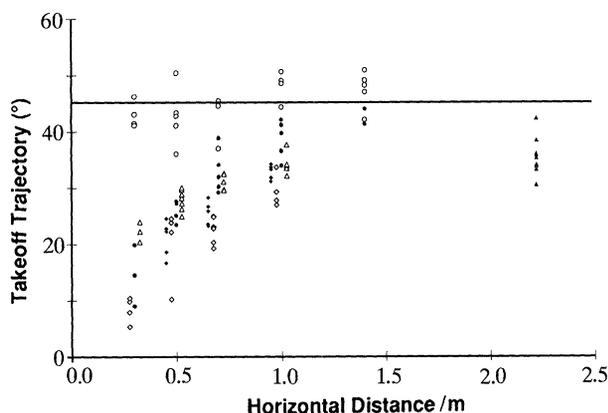


Figure 2. Jump takeoff angles for jumps of different lengths for *C. major* (filled circles), *G. moholi*, (open circles), *G. garnettii*, (filled diamonds), *Mirza coquereli* (open triangles) and *Microcebus murinus* (open diamonds) and for a 2.25-metre jump for *L. catta* (filled triangles).

bancanus. However, we found that, for *G. moholi*, jumps with an effective distance over 1.6 m were made from larger initial supports than were shorter jumps. Secondly, in *T. bancanus*, the longest jumps end on supports which are significantly larger than for the two shortest jump categories. Further, we found that longer jumps, above 0.8 m in the bushbabies and above 1.6 m for the tarsier, result more often in height gain, but shorter jumps result more often in height loss (Duncan's multiple range test, $p < 0.05$ in each case). We found no significant relation between initial and terminal support orientation and leap distance.

Analysis of the trajectory of the body centre of gravity gave the results plotted in figure 2. This graph shows that at the shorter distance no species except for *G. moholi* adopts the energy-efficient angle of 45° . However, as jump length increases, the animals adopt increasing angles, all species (except *L. catta* for which only one distance was filmed) tending to approach the 'optimal' takeoff angle of 45° at the maximum jump that could be elicited from them by a food reward.

4. DISCUSSION

It might be argued that our findings on support usage reflect only the availability of supports of different diameters in different forest strata. Indeed, support

diameter was found to be negatively correlated with height in the *Galago* studies (Crompton 1984), longer jumps occur more often at low heights in *G. moholi*, and longer jumps ended on significantly higher terminal supports for *G. crassicaudatus*. But if our findings on leap length and diameter were merely a product of stratum differences, these relations should be symmetrical for initial and terminal supports. This was not the case in any of the three species examined.

Our field results suggest that *G. moholi* at least may avoid losing energy to the takeoff support in longer jumps by selecting takeoff supports of larger diameter and hence lower relative compliance. An alternative explanation of this finding is that these large-diameter supports are selected as stiff external energy stores, into which the bushbaby 'pumps' energy before the thrust phase of takeoff. However, stiffness consequent on the large diameter (4–6 cm) and limited free length (< 1.5 m) of supports used in the longer leaps (Crompton 1980, 1984; Crompton & Andau 1986) would probably be excessive for their use as an energy store by a 240 g *G. moholi*, even at the peak reaction force of $12.5 \times$ body weight recorded by Günther (1989). It is with larger saltatory primates (with longer hindlimbs, and hence a longer takeoff duration in comparison with the natural frequency of the support) that we should expect to find external storage of energy.

For *T. bancanus*, our evidence for selection of larger diameter terminal supports seems to allow no other explanation than selection of more stable targets. *Tarsius* (like *G. moholi*) lands feet first, with extended legs, which can dissipate the landing force during flexion. For this small-bodied species, therefore, the stability of its target may be of more concern than the possibility of dissipating energy as jump length increases. In *G. crassicaudatus*, which is ten times larger, always landing forelimb first (Crompton 1980) and thus less able to use the long hindlimbs as a shock absorber, we found that terminal supports in the longest jumps are significantly smaller in diameter than for all shorter jumps, so the potential for dissipation of energy through the support is present for the species which needs it most.

On energetic grounds, we expected that longer leaps would result in height loss, as animals get nearer to

their maximum effort. However, the contrary was the case in all three species. This unexpected result might be explained by tendencies, both to avoid the lack of control and increased mechanical forces, which might result from the acceleration due to gravity that would occur in the second half of a downwards-directed parabolic leap, and to use gravity to slow the body before landing in an upwards-directed leap.

In our study, only *G. moholi* always took off at the optimum angle of 45°. Available kinematic analyses of the leap of *T. bancanus* (Niemitz 1984; Peters & Preuschoft 1984) suggest that it follows *G. moholi* in this regard. The equation

$$V_x = \cos \theta \sqrt{(rg/\sin 2\theta)}, \quad (3)$$

derived from equations (1) and (2) above, gives the horizontal speeds achieved with different takeoff angles. Plotted in figure 1, for a 1 kg animal, these show that jumps with higher takeoff trajectories have a slower horizontal speed. Jumping, optimized for distance, is thus not a very fast means of locomotion. It typically occurs at velocities of some 4 m s⁻¹, compared with ground speeds of up to 15 m s⁻¹ achieved by cursorial quadrupeds (Günther *et al.* 1991), and, all other things being equal, is thus not as effective a means of travel.

For *G. moholi*, however, jumping remains of far greater importance than quadrupedalism (walking and running) as a means of travel (53% against 20% of all displacements, and 672 m against 173 m of every kilometre of travel (Crompton 1980, 1984)). The configuration of the limb segments appears to be such that the performance improvements that can be made in quadrupedal locomotion are severely limited (Smith 1987). Primate quadrupeds such as the stump-tailed macaque and hamadryas baboon can achieve maximum mass-specific aerobic oxygen consumption rates (V_{O_2} max.) of 1.598 ml kg⁻¹ s⁻¹ at 5.0 kg body mass, and 1.456 ml kg⁻¹ s⁻¹ at 8.5 kg, respectively (Taylor *et al.* 1982). A regression of Taylor *et al.*'s V_{O_2} determinations on 20 species by Lindstedt *et al.* (1991) predicts that a 240 g *G. moholi* should be able to achieve a maximum of 2.55 ml kg⁻¹ s⁻¹. However, Taylor *et al.* measured the actual maximum performance of three *G. moholi* at 1.15 ml kg⁻¹ s⁻¹, less than half the predicted value. Substantial improvements in travel speed thus cannot be made by quadrupedalism, and where speed is at a premium it is not a viable alternative to jumping.

Jumping, moreover, offers a means of crossing large discontinuities, and thus an escape from detours (Crompton 1980, 1984). Consideration of the number and complexity of limb segment excursions involved suggests to us that, although jumping locomotion is certainly more expensive than walking, running or galloping, climbing would be more expensive yet – as a means of gaining or losing height – particularly for any small-bodied arboreal species. Where detours would entail climbing, therefore, jumping *per se* probably becomes an energy-efficient choice. Indeed, field data show that climbing is not adopted as a primary means of changing height during travel by either *T. bancanus* or *G. moholi* (Crompton 1980, 1984; Crompton &

Andau 1986). Height change is accomplished by jumping, climbing occurring most often in the context of 'detailed foraging' or active searching for food.

For the less frequent leapers, *G. garnettii*, *L. catta* and the cheirogalaeines, the question is rather, why do they not jump at the energy-efficient takeoff angle of 45° until they are nearing their maximum range? For, to take off at low angles, these species have to reach higher velocities and have to exert much higher muscle forces – and hence tolerate higher loads – as well as spend more energy. One explanation might be that they have higher 'metabolic efficiency' than the small species: however, available anatomical data (Grand & Lorenz 1968; McArdle 1981; Crompton 1982, Peters and Preuschoft 1984; Smith 1987; Günther 1989) strongly suggest that, in *T. bancanus* and *G. moholi*, muscle arrangement, segment inertial properties and body motion are more optimally configured for leaping than in the other species, including, very significantly, the even smaller *Microcebus murinus*. Body size alone, therefore, does not account for the differences observed in takeoff trajectories: the smallest and the largest species in our study, *Microcebus murinus* and *L. catta*, both leap at less than the energetically optimal angle.

Jumps at low angles have the advantage, at any distance, of short duration. The combination of short duration and flat trajectory might make it more difficult for a predator to predict the path of potential prey. However, *L. catta* and *G. garnettii* are too big to be at much risk as an adult. The latter species, and all three cheirogalaeines, live in the middle levels of the forest, where vegetation is fairly dense, and the risk from predators is minimized (Oxnard *et al.* 1990). Discontinuities here are typically numerous but short, so that long jumps are not required. *G. moholi* and *T. bancanus*, however, spend a considerable amount of time near ground level, where discontinuities are few but large (Crompton 1984; Crompton & Andau 1986). However, predation risk may be higher both in parabolic trajectories and in this open arboreal zone where such trajectories can most easily occur. Although jumping itself may be a safer means of movement here than quadrupedalism, for high-trajectory, low-speed jumps to be preferred over low-trajectory, high-speed jumps, the benefits of energy efficiency must outweigh the risk of predation.

5. CONCLUSIONS

In our experimental study, only the anatomically 'specialized' jumper, *G. moholi*, for which behaviour, body proportions and muscular anatomy are optimized for leaping, seems to adopt energy-efficient paths at all jump distances. Available evidence suggests that *T. bancanus* does the same. In field studies, however, only *G. moholi*, of the two specialized jumpers, appeared to follow the expectation for energy optimization in selecting larger, less compliant supports for takeoff in longer jumps: interestingly, this is the less specialized, behaviourally and anatomically, of the two. For *T. bancanus*, although energetic costs and musculoskeletal loads may well have brought about its very specialized configuration, the stability of the target substrate now

appears as important as the benefits of elastic storage or dissipation of energy through the support. In-flight body rotation in such specialized jumpers enables the hindlimbs to dissipate as well as to generate force.

However, for the unspecialized *G. crassicaudatus*, there is evidence that musculoskeletal loads are important considerations; target supports appear to be selected for greater compliance on the longest leaps. For most unspecialized species, moreover, energy efficiency may be less important than ecological factors. The ecological advantage of flat, energetically inefficient trajectories for these species may instead be related to the ease of movement through dense vegetation in which a high parabolic trajectory would be hazardous (see Charles-Dominique 1977). The complexity and instability of the arboreal habitat thus seems to be as significant an influence on locomotor behaviour as any tendency to minimize the energetic costs and forces involved in locomotion.

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