
REVIEW

BRANCHING OUT IN LOCOMOTION: THE MECHANICS OF PERCH USE IN BIRDS AND PRIMATES

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Accepted 9 March; published on WWW 6 May 1999

Summary

Many animals use thin perches, such as the branches of trees, as locomotory substrates. In this paper, I have reviewed the literature concerned with measurements of locomotory forces made by birds and primates on thin and flexible substrates. Through a knowledge of the locomotory forces exerted by animals when using different substrates, the mechanical cost of their use can be established. We are just beginning to learn about the magnitude and patterns of force production in various branch-using vertebrates, primarily as a result of the development of instrumented perches. Instrumented perches have been designed to measure the forces produced by birds and primates when leaping from rigid and flexible horizontal and flexible vertical perches, and also from instrumented handgrips during brachiation. The development of these techniques

for birds and primates allows us to compare the way in which they use perches as locomotory substrates.

In both birds and primates, the magnitudes of landing forces are smaller than those during take-off. Two explanations have been proposed; the difference is either a consequence of perch compliance or it is a strategic decision to be cautious of 'new' perches. Leaps from flexible perches may be somewhat inefficient because considerable energy is dissipated in bending the perch, and this energy may remain unrecovered when the animal leaves contact with the perch.

Key words: bird, primate, perch, biomechanics, take-off, landing, locomotion, force.

Branches as locomotory substrates

We are all familiar with seeing birds perching on the branches of trees and other thin substrates such as power lines. Little is known about how birds utilise such substrates during landing, take-off and walking. Observing birds in the field, it is apparent that most, to a greater or lesser degree, use leg thrust to propel themselves upwards and forwards during take-off before the completion of the first wingbeat cycle (Heppner and Anderson, 1985; Bonser and Rayner, 1996). Birds, of course, are not the only vertebrates to use such substrates during locomotion; primates in particular are adept at moving in the tree canopy using branches as locomotory substrates. Primates use branches as locomotory substrates in different ways; they may walk along them, leap to and from them or brachiate between them. Recently, the kinematics of primate running on and leaping from thin perches has been examined (see Schmitt, 1994; Demes et al., 1996), but estimates of force production are required so that the mechanical cost of using different substrates can be determined. In this paper, I will review how such forces have been measured.

Until recently, few attempts had been made to measure force production when animals leap from perches or use them as locomotory substrates. Although flat force plates have had a

long history of use and have been well-developed (see Cavagna, 1985), they are not entirely suitable for measuring locomotory forces from perches. Force plates are rigid, whereas perches and branches are flexible, so losses of elastic energy do not occur. Additionally, animals must grip and balance on perches, so the influence of maintaining stability and posture is greater when an animal uses a thin and compliant substrate.

By using methods of measuring locomotory forces, it is possible to determine the total mechanical energy requirements of locomotion (Cavagna, 1985; Blickhan and Full, 1992). The results of such studies will enable us to determine the costs and benefits of locomotory strategies. In this review, I will draw together the current literature on the mechanics of perch use by birds and primates.

Mechanical measurement methods

Birds

Early attempts to measure the leg thrust forces of birds during take-off and landing were made by Fisher (1956a,b). Fisher's (1956b) method used a flat mechanical force plate capable of

resolving vertical, horizontal and lateral forces. The first attempt to measure take-off leg thrust in birds from instrumented perches was made by Heppner and Anderson (1985). A perch was fixed to a load cell, enabling the vertical force component of leaps to be measured. Using this device, the leg thrust forces produced by pigeons (*Columba livia* Gmelin) during take-off were measured. Recently, Bonser and Rayner (1996) designed and constructed a more sophisticated system which enabled both the vertical and horizontal force components of leaps made by starlings (*Sturnus vulgaris* L.) to be measured. Their instrumented perch used perpendicular flat blades, with strain gauges attached, as force transducers in a similar manner to that used in flat force plates (see Heglund, 1981). A set of two transducer blades was attached to each end of a rigid wood perch. Leg thrust forces were measured during take-off and landing in starlings. In a further development of this technique, Bonser et al. (1999) went on to construct a series of cantilevered perches of varying diameter, which enabled them to measure leg thrust forces on perches of varying flexibility.

Primates

Methods have been developed to examine the mechanical forces primates produce when leaping from flexible branches. Demes et al. (1995) constructed a flexible, instrumented pole from which to record leaping and landing forces in primates.

Primates do not move from branch to branch solely by leaping. Many species use branches as substrates for brachiation. Chang et al. (1997) developed a transducer to measure forces in swinging arm locomotion, which they then used to measure locomotory forces in gibbons (*Hylobates* spp.). By using a cross of instrumented beams attached to a handhold, they were able to measure moments applied in the three orthogonal axes. This force transducer system was mounted as one component of an aerial trackway of handgrips. This arrangement allowed force measurements to be made when gibbons brachiated between them.

Transducer design

The studies reviewed above have, principally, used either single- or twin-bladed force transducers. Heglund (1981) describes the principles of construction of single-bladed designs, and design considerations for twin-bladed transducers are given by Biewener and Full (1992). In this section of the paper, I will discuss briefly the design of such transducers and the advantages and disadvantages of both methods. Briefly, blades are machined in a piece of metal, and electrical strain gauges are attached to them. Thin blades flex in the desired direction of measurement (horizontal or vertical), and the resistance of the gauges varies in proportion to the strain applied to them. A suitable amplifier enables these changes in resistance to be output as a voltage. Fig. 1 shows the design of single- (Fig. 1A) and twin- (Fig. 1B) bladed force transducers for perches. The blade width, d , and thickness, t , are referred to in the equations that follow. The blades should be as thin as possible to allow the maximum change in strain gauge resistance and hence sensitivity; however, under no

circumstances should the blade be so thin as to undergo plastic deformation (yielding) when in use. The following equations allow the minimum permissible blade thickness to be calculated.

To begin with, I will consider how a beam behaves under loading. Let us consider the mechanical behaviour of a prismatic beam first. The stress, σ , at the surface of a member is given by:

$$\sigma = \frac{My}{I}, \quad (1)$$

where M is the applied bending moment, I is the second moment of area of the beam section, and y is the distance from the neutral axis of the section to its outermost surface. In the case of square sections and single blades, the second moment of area, I , is given by:

$$I = \frac{dt^3}{12}, \quad (2)$$

where d is the breadth and depth of the beam and t is its thickness. By using equations 1 and 2, the ideal thickness for the transducer blade can be calculated. Heglund (1981) suggests that a factor of safety of 14 is appropriate for the design of force transducer blades. The maximum allowable stress in the transducer blade must not exceed the yield stress of the blade material, so

$$t = \sqrt{\frac{6M}{d\sigma}}. \quad (3)$$

However, if using a twin-bladed design, I is given by:

$$I = \frac{d}{12} [d^3 - (d - 2t)^3], \quad (4)$$

where d is the depth of the beam and t is the thickness of the blade. Substituting this equation for I in equation 1, we find that blade thickness is given by the solution of the polynomial:

$$0 = \frac{2dt^3}{3} - d^2t^2 + \frac{d^3t}{12} + \frac{Md}{\sigma}. \quad (5)$$

Biewener and Full (1992) give only the equations for the behaviour of a single, isolated blade. The two blades of a twin-bladed design cannot be considered to act independently, so equation 5 (above) rather than the single-blade equation (equation 3, above) should be used to calculate blade thickness.

Whatever design of transducer is selected, it must satisfy several criteria: (1) crosstalk between forces in each direction should be minimal, (2) the material of the blades should not undergo strains close to yield, (3) the beams should be designed to give a good deflection for the required range of loads, and (4) the natural frequency of the transducer should not be close to the expected frequency of the loading events.

It should be noted that the above equations refer only to the strength and stiffness of the transducer blades themselves. The overall stiffness and strength of instrumented perches also

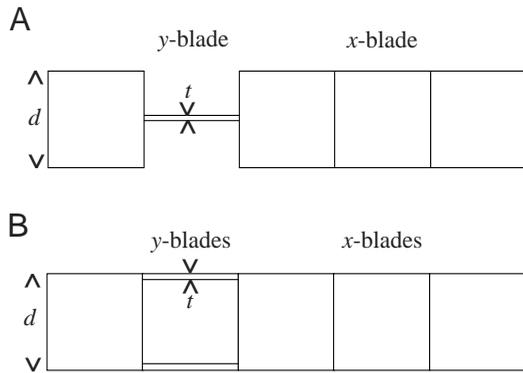


Fig. 1. Side view of transducer blades for single-bladed (A) and twin-bladed (B) force transducers. d is the blade thickness and t its thickness (see equations 2–5). y - and x -directions are vertical and horizontal, respectively.

depend on the properties of the perch. As we will see later in this paper, this can be used to the investigator's advantage to determine how animals change their behaviour in response to variations in substrate properties.

Force production

Birds

The hindlimb anatomy of birds suggests that they should be efficient jumpers: Alexander (1995) proposes that long legs and extended tarsal bones are indicative features. At present, there are data from only two species of bird on leg thrust forces. Heppner and Anderson (1985) found that the vertical force components during pigeon take-off were 1.3–2.3 times body weight (4.83 ± 0.93 N; mean \pm s.d., $N=16$). Unfortunately, their apparatus could not measure horizontal force components, so the magnitude and angle of the resultant force could not be calculated.

The paper of Bonser and Rayner (1996) provided data on both landing and take-off forces in common starlings (*Sturnus vulgaris*). Their perch measured both the horizontal and vertical force components, which allowed the magnitude and direction of resultant leg thrust forces to be calculated. Their experiments revealed interesting results concerning the differences between landing and take-off angles and forces. There was a significant difference between the forces during landing and take-off; take-off forces were some 45% higher than during landing. There was no significant difference in the angle of the resultant force. Take-off forces were 2.6 times body weight, and those during landing 1.8 times body weight. Both landing (F_L) and take-off (F_T) forces (N) scaled linearly with body mass (M , g): $F_L = 59.54M - 2.993$ ($r^2 = 0.365$, $N=213$, $P < 0.001$); $F_T = 58.83M - 2.388$ ($r^2 = 0.387$, $N=202$, $P < 0.001$). However, there was no relationship between the angle of the resultant force and body mass. Force traces obtained in this study showed some interesting features; during take-off, there was an apparent decrease in the force exerted by the bird on the perch just prior to leaping. The presence of this 'unweighting' event is indicative of the bird dropping to a

crouched posture; this may increase the energetic efficiency of leaping, because countermovement jumps are both more energetically efficient and higher than squat jumps (Anderson and Pandey, 1993; Voigt et al., 1995; Alexander, 1995).

One feature of Bonser and Rayner's (1996) results was that the repeatability (Harper, 1994) of angles was low. Bonser and Rayner (1996) suggested that this may be a mechanism of making the initial trajectory of a bird unpredictable and, hence, confusing to potential predators. The birds had only two perches, so variability in trajectory due to birds having varying destinations would be unlikely. This hypothesis is supported by work on the escape responses of fish. Domenici and Blake (1993) found that, although escape trajectories were directed away from a startle stimulus, there was a multiple preferred range of trajectories.

In a subsequent paper, Bonser et al. (1999) used flexible force-transducing perches to investigate whether substrate properties influence take-off behaviour; the results of this work will be discussed fully later in this review.

Primates

Demes et al. (1995) examined the landing and take-off forces produced by primates. They found that landing forces were considerably lower than take-off forces. Take-off forces were 9.6–10.3 times body weight, whereas landing forces were 6.7–8.4 times body weight. They argued that take-off forces were higher than those during landing because the kinetics of landing determined take-off strategy.

In studies considering the take-off and landing behaviour of birds and primates, there has been a similarity in the patterns of results that have been obtained. Both Demes et al. (1995) and Bonser and Rayner (1996) reported that take-off forces were significantly higher than landing forces. Demes et al. (1995) suggested that landing forces are lower because compliant substrates absorb energy. Bonser and Rayner (1996) suggested that, in birds, the discrepancy is due to animals being circumspect. In a recent paper, Green and Cheng (1998) reported that, when faced with a novel perch, pigeons increase their approach velocity and maximum landing force on repeated landings. Birds can flap their wings to decelerate, whereas primates obviously do not have this facility, allowing birds much more control of their landing mechanics. There is some evidence, however, that primates do not behave aerodynamically as a projectile; they may have some control over their aerodynamic performance. Demes et al. (1991) found that prosimian primates are able to improve their aerodynamic performance by changing their posture during flight. This enabled them, for example, to make longer leaps than would otherwise be predicted: clearly, primates are capable of adjusting their flight speed, but not to the same extent as birds.

Initial results from studies of brachiation (Chang et al., 1997) have revealed that the peak forces exerted on a substrate occur during the midpoint of a swinging cycle. The peak magnitude of these forces is almost twice the animal's body weight. The force records from brachiation show that force varies sinusoidally from initial hand/handgrip contact to

release. It is interesting to note that studies of functional strain in the limb bones of spider monkeys (*Ateles* spp.) have revealed that the highest locomotory strains occur during the support phases of quadrupedal locomotion; strains during brachiation are markedly lower (Fleagle et al., 1981). Recent studies of functional strains in primate limbs have not addressed the question of how strains vary during different modes of locomotion within individuals. Swartz et al. (1989) measured strains in the arm bones of brachiating gibbons and concluded that tensile strains were more likely to be present than during walking. Demes et al. (1998) examined walking and galloping, but neither jumping nor climbing. Clearly, an urgent priority for researchers measuring functional strains in primate limbs must be to compare the strains in bones during different modes of locomotion in the same individual.

Substrate properties and behaviour

It may be expected that differences should be observed in the take-off and landing behaviour of animals faced with perches of differing properties. Branches of trees act as cantilevers; they are fixed at one end and free to deflect at the other. As a result, they are more compliant and weaker than perches fixed at both ends. The compliance and strength of cantilever perches are dependent upon the cross-sectional shape and perch length (Gordon, 1976). The deflection, δ , of a cantilever perch, loaded at its tip, is given by:

$$\delta = \frac{Pl^3}{3EI}, \quad (6)$$

where P is the applied load, l is the length of the perch, E is the Young's modulus of the perch and I is its second moment of area. Compliance, that is the amount a perch deflects under loading, is simply deflection, δ , divided by load, P . The strain energy, U , stored by a cantilever perch is given by:

$$U = \frac{P^2l^3}{2EI} \quad (7)$$

(Gere and Timoshenko, 1991), so it becomes apparent that the energy stored in a perch is proportional to P^2 . If we vary the radius, r , of the perch, I will change. The value of I increases with the fourth power of r , so we can see that increasing the perch radius will dramatically decrease the energy capable of being stored.

Of course, changing the diameter of a perch will also have an effect on its strength. The peak mechanical stress, σ , on a perch is given by:

$$\sigma = \frac{Plr}{I}, \quad (8)$$

so thinner perches are weaker than thick ones. The 'safety factor' in the design of the perch is simply the ratio of the stress imposed upon it to the failure stress of wood.

In birds, only one study has sought to examine the effect of substrate properties on locomotory performance. Bonser et al. (1999) devised a series of instrumented perches of varying

diameter. Compliance varied by a factor of 390 and strength by a factor of 87 between the smallest and largest perch. Somewhat surprisingly, there was no significant difference between the forces the birds exerted on each perch. As a result, the safety factor of the perch was between 2.83 and 250.35, and there was a 390-fold difference in energy absorbed by the perch.

The measurements of landing and take-off forces made by Demes et al. (1995) on primates showed that perch compliance has an effect on the leaping performance. They found that perch-increased compliance tends to increase take-off forces and decrease landing forces. These results differ from those of Bonser et al. (1999), who reported no change in take-off forces when starlings were faced with perches of varying flexibility. It is curious that primates, when faced with a perch of low strength, increase the forces to which they subject thin perches, hence increasing the likelihood of them failing. In starlings, perch safety factor decreases in proportion to the dimensions of the perch, but in primates it decreases at a higher rate, because they tend to produce higher forces on thinner perches during take-off. At present, there are no data concerning the effects of perch thickness on landing forces in birds.

Can animals recover elastic energy stored in substrates? Alexander (1991) does not consider that animals can recover this energy. Theoretically, if the natural frequency of a perch is high enough, an animal may be able to use stored elastic energy (Crompton et al., 1993). Indeed, Bonser et al. (1999) observed that perches continue to oscillate after a bird has left the perch, so much of the energy presumably remains unrecovered. Demes et al. (1995) suggested that, in primates, elastic energy stored in perches is wasted, since the animals were observed to take off before the perch recoiled. It would seem that, whilst animals store elastic energy in muscles and tendons (Alexander and Bennet-Clark, 1977; Biewener et al., 1981), they do not utilise energy stored in locomotory substrates. Behavioural observations have indicated that prosimian primates tend to choose rigid perches when they wish to make long leaps (Crompton et al., 1993), hence minimising the wastage of energy in perch deflection. Interestingly, lemurs (*Lepilemur* spp.) (Warren, 1997) and starlings (Cuthill and Witter, 1994) prefer small or intermediate-sized perches, but this may be due to comfort rather than elastic efficiency. The ability to grip a perch comfortably may be important in determining how efficiently an animal can use it. Certainly, there is evidence that humans are more effective at gripping objects with particular hand spans (e.g. Petrofsky et al., 1980; Fransson and Winkel, 1991). These initial studies of locomotion using compliant substrates superficially indicate that animals take little regard of substrate properties. More detailed analyses of kinematics and force production may tell us more about the energetics of using compliant substrates. If the moments acting on joints during leaping are determined, it may be possible to calculate the muscular forces produced; this will enable a more realistic estimate of the energetics of using compliant substrates to be made.

While decreasing perch thickness increases the potential for elastic energy storage, there is a concomitant increase in the risk of a perch failing. It appears that animals will subject their

perching substrates to much lower safety factors than that to which they will customarily subject their skeletons. Alexander (1981) found that animals' skeletons work within a range of safety factors of 2.5–6; however, Bonser et al. (1999) found that the leg thrust force exerted by starlings is sufficient to reduce the safety factor of their substrate to similar values. It could be argued that this is a risky strategy: if a perch fails, the animal may collide with other branches or even fall to ground. The risk of injury is likely to be higher for primates than for birds, since birds are able to commence flight to prevent hitting obstructions whereas primates clearly cannot. In either event, there is a high probability that the animal may sustain mechanical damage (e.g. bruising, fracture of limb bones, broken feathers or damage to internal organs). Reports in the literature of the frequency of healed limb bone fractures indicate that they are not rare occurrences; Schultz (1939), for example, found that of 118 gibbons sampled, 48 had evidence of healed limb bone fractures. The use of instrumented flexible perches may enable us to learn more about how animals assess the mechanical competence of their locomotory substrates.

I wish to thank Dr Adrian Thomas and two anonymous referees for their suggestions for improvements and Sheila Knight for improving the readability of this manuscript.

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