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# Orangutans use compliant branches to lower the energetic cost of locomotion

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Within the forest canopy, the shortest gaps between tree crowns lie between slender terminal branches. While the compliance of these supports has previously been shown to increase the energetic cost of gap crossing in arboreal animals (e.g. Alexander 1991 *Z. Morphol. Anthropol.* 78, 315–320; Demes *et al.* 1995 *Am. J. Phys. Anthropol.* 96, 419–429), field observations suggest that some primates may be able to use support compliance to increase the energetic efficiency of locomotion. Here, we calculate the energetic cost of alternative methods of gap crossing in orangutans (*Pongo abelii*). Tree sway (in which orangutans oscillate a compliant tree trunk with increasing magnitude to bridge a gap) was found to be less than half as costly as jumping, and an order of magnitude less costly than descending the tree, walking to the vine and climbing it. Observations of wild orangutans suggest that they actually use support compliance in many aspects of their locomotor behaviour. This study seems to be the first to show that elastic compliance in arboreal supports can be used to reduce the energetic cost of gap crossing.

**Keywords:** compliance; energy expenditure; locomotion; orangutan

## 1. INTRODUCTION

Branch compliance presents a major problem for arboreal animals that travel and feed in the forest canopy. Branches taper towards their ends, but the narrowest gaps between trees are situated between the thin terminal branches of adjacent tree crowns. Efficient travel through the rainforest canopy requires animals to minimize the deviations from their travel path, unless such deviations are more energetically efficient than direct travel (although non-energetic factors such as the risk of falls may also influence gap-crossing decisions). In theory, compliant terminal branches may act as external springs adding momentum to jumps and leaps across gaps, but most researchers have suggested that compliant supports increase the cost of arboreal locomotion. Alexander (1991) showed that quadrupedal monkeys lose energy during take off and landing as branches bend under their

weight and jumping lemurs generally lose contact with branches before they recoil, expending energy to deform supports but failing to exploit the elastic energy to aid momentum (Demes *et al.* 1995). However, field observations suggest that some primates can use branch compliance to their advantage: galagos and pygmy chimpanzees (*Pan paniscus*) use branches as catapults (anecdotal evidence cited in Demes *et al.* 1995) and various species pump branches prior to leaps to make use of the propulsive force of branch recoil (Cant 1994). Recent studies of orangutans offer increasing evidence that many aspects of their gap-crossing behaviour use elastic energy stored in compliant branches (Cant 1987, 1994; Thorpe & Crompton 2005, 2006), even though their large body mass might be expected to render arboreal gap crossings energetically costly and a safety risk. The best documented example of orangutans using support compliance is tree sway, in which individuals oscillate thin vertical tree trunks with increasing magnitude until a support on the opposite side of the gap may be reached (e.g. Cant 1987; Thorpe & Crompton 2006).

Clearly, arboreal primates differ markedly in their response to branch compliance and such variability is likely to have been central to evolutionary radiations of the order (Cant 1994). To date, however, no study has compared the energetic efficiency of alternative methods of crossing gaps in the forest canopy. In this paper, we will calculate the energetic cost of tree sway, jumping and descent/ascent during gap crossing in orangutans (*Pongo abelii*) to address the hypothesis that the use of energy stored in compliant supports enables energetically efficient gap-crossing behaviour for arboreal primates.

## 2. MATERIAL AND METHODS

The energy cost of crossing a gap by tree swaying can be estimated from videos. It is seldom possible to get unobstructed views of apes crossing gaps between forest trees, but suitable videos were obtained at an exceptionally favourable location in the Gunung Leuser National Park, Sumatra, Indonesia during a year-long study of wild and rehabilitant orangutan locomotion (for full methods, see Thorpe & Crompton 2005). The area was near a feeding platform where free-ranging rehabilitants congregated daily for food supplements. Wild males also congregated at the feeding station, but did not receive food. Orangutans repeatedly crossed from the vertical trunk of a young tree to a vine that was out of reach, by swaying the tree. Calibration of the height of the animal on the sapling and the amplitude of the vibrations was possible from the measurements made on support lengths and diameters at ground level. Video sequences were recorded with a digital video camera (Sony DCR-TRV 900E) at a speed of 25 frames per second.

## 3. RESULTS AND DISCUSSION

### (a) Calculations of energy expenditure

Consider an orangutan at point *P* on the trunk of a sapling, who wishes to move to a nearby sapling or vine that is out of reach by a distance *d* (figure 1). It makes its sapling vibrate at its resonant frequency, building up the amplitude to the value *d* that enables it to move across.

Free vibrations of the sapling continue after the ape has left it. The motion of point *P* can be modelled as that of a linear, lightly damped harmonic system, in which case the frequency, *f*, of the vibrations is given by

$$f \sim (1/2\pi)\sqrt{(S/m)}, \quad (3.1)$$

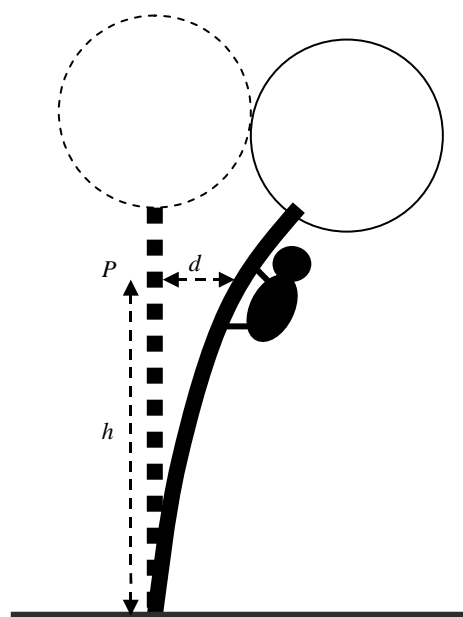


Figure 1. Mechanics of tree sway.  $P$  is the position of the orangutan at height  $h$  from the ground and  $d$  is the distance the animal must vibrate the sapling to cross the gap.

(e.g. Alexander 1983), where  $S$  is the stiffness of the sapling to horizontal forces applied at  $P$  and  $m$  is the effective mass (the mass which, located at  $P$ , would have the same inertia as the tree). Rearrangement of this equation gives the stiffness  $S$  (assumed, for simplicity, to be constant)

$$S \sim 4\pi^2 f^2 m. \quad (3.2)$$

Previously, when the ape was still on the tree, the stiffness was the same but the effective mass was  $(m+M)$ , where  $M$  is the mass of the ape. The ape presumably vibrated the tree at the resonant frequency. When damping is light, the resonant frequency is approximately equal to the frequency of free vibration, so

$$S \sim 4\pi^2 F^2 (m+M). \quad (3.3)$$

From equations (3.2) and (3.3), we can obtain an equation for the effective mass,  $m$ , of the tree

$$m \sim MF^2/(f^2 - F^2). \quad (3.4)$$

The frequencies  $F$  and  $f$  can be measured from videos, and the masses  $M$  of the apes can be estimated with reasonable confidence (after Markham & Groves 1990).

The assumption that damping was negligible requires justification. A damped free vibration decays with half-cycle logarithmic decrement  $\delta$ ,

$$\delta = \log_e(d_n/d_{n+1}), \quad (3.5)$$

(eqn (7.7), Alexander 1983), where  $d_n$  and  $d_{n+1}$  are the amplitudes of the motion half a cycle apart. We determined  $\delta$  for the tree in question from the measurements of the amplitudes of five successive cycles of the decaying vibration after the ape had left, and obtained a value of 0.073. It can be shown from eqns (7.6) and (7.7) of Alexander (1983) that damping can be ignored in equations (3.2) and (3.3)

(above) if  $\delta^2$  is very small compared with  $\pi^2$ . Our measurement shows that this was the case.

Thus,  $S$  and  $m$  can be obtained from equations (3.2) and (3.4). This makes it possible to estimate the strain energy in the tree when point  $P$  is displaced a distance  $d$  from its equilibrium position. As the stiffness is assumed to be constant

$$\text{Strain energy} = \frac{1}{2} S d^2. \quad (3.6)$$

The work that the ape must do, to make the crossing, is the sum of two components:

- (i) The strain energy  $1/2(Sd^2)$  stored in the tree, when the ape is just able to reach the one it wants to move to.
- (ii) The energy dissipated by damping, in the series of vibrations in which the amplitude is built up. Though the damping was light enough to be ignored in the calculations of stiffness and effective mass, it may be significant in this context.

The energies of successive half cycles of free vibration, estimated as peak strain energy, are proportional to  $(d_{n+1}/d_n)^2$  and so to  $[\exp(\delta)]^{-2}$ . Thus, damping dissipates a fraction  $1 - [\exp(\delta)]^{-2}$  of the current energy of the vibration in each half cycle. With  $\delta = 0.073$ , as observed, this is 0.14 of the energy. The fractional viscous energy loss per half cycle  $\Delta$ , as the ape builds up the vibrations, is less than this because the frequency is lower, making velocities lower for a given amplitude.

$$\Delta = (F/f)\{1 - [\exp(\delta)]^{-2}\}. \quad (3.7)$$

Consider an ape building up vibrations in a tree over  $(n-0.5)$  half cycles. For simplicity, assume that the energy of the vibration is increased by the same factor, in each half cycle, to the required value  $1/2(Sd^2)$ . In each half cycle of a vibration, a fraction  $\Delta$  of the current energy of the vibration is lost. Thus, the total energy dissipated by damping is  $1/2(Sd^2)\Delta[1/n + 2/n + 3/n + \dots + (n-1)/n + 0.5] = 1/2(Sd^2)(n\Delta/2)$ , and the total work requirement for the manoeuvre is

$$\text{Work} = \frac{1}{2} S d^2 [1 + (n\Delta/2)]. \quad (3.8)$$

Table 1 shows that the work calculated in this way is only a little greater than the peak strain energy. Damping is not very important for the energetics of the manoeuvre.

The lower stiffness and effective mass of the tree in sequence 3, than in sequences 1 and 2, are due to the ape's position  $P$  being higher. If the tree trunk had been a uniform cylinder, its stiffness would have been inversely proportional to the cube of the height of  $P$  (see eqn (4.3), Alexander 1983). As it tapered, its stiffness must have fallen even more rapidly with increasing height. We can only roughly estimate the heights from the ground, but the difference of height seems consistent with the difference of stiffness. (In table 1, the stiffness calculated for sequence 3 is 0.9 of the value that would have been predicted from sequence 1 on the assumption of inverse proportionality

Table 1. Results for three passages of orangutans across the same gap between a sapling and a nearby vine.

video sequence number	1	2	3
<i>description of animal</i>	<i>rehabilitant mother</i>	<i>rehabilitant mother with infant</i>	<i>wild subadult male</i>
estimated mass of animal, $M$ (kg)	40	43	55
estimated height from ground, $h$ (m)	7.2	7.1	7.9
maximum amplitude, $d$ (m)	0.61	0.58	1.46
frequency of forced vibrations, $F$ (Hz)	0.49	0.51	0.37
frequency without ape, $f$ (Hz)	0.88	0.89	(0.88)
half-cycle logarithmic decrement, $\delta$	0.073	(0.073) <sup>a</sup>	(0.073)
stiffness of tree, $S$ (N m <sup>-1</sup> )	550	657	361
effective mass of tree, $m$ (kg)	18.0	21.0	11.8
peak strain energy, $1/2(Sd^2)$ (J)	102	111	385
fractional half-cycle energy loss, $\Delta$ , as vibrations are built up (equation (3.7))	0.08	0.08	0.06
number of half cycles, $(n-0.5)$	3.5	4.5	4.5
work required (kJ; equation (3.8))	0.12	0.13	0.44
work for a jump (kJ; equation (3.10))	0.25	0.25	1.31
work to climb to height, $h$ (kJ)	2.8	3.0	4.3

<sup>a</sup> Data in parentheses could not be measured on the sequence in question, but can be assumed to be the same as for sequence 1.

to the cube of estimated height.) The effective mass is of course proportional to the stiffness, as the frequency of vibration after the ape has left (equation (3.1)) is independent of the height of  $P$ .

Table 1 shows the work required for making the tree sway, estimated in this way from videos of three crossings of the same gap. The gap could alternatively have been crossed by jumping or descending the tree, walking to the vine and climbing it. How do the energy costs of these alternatives compare?

An animal taking off at 45° to the horizontal to jump a distance  $d$  requires a velocity  $\sqrt{(dg)}$ , where  $g$  is the gravitational acceleration (e.g. Alexander 1983). If its mass is  $M$ , the horizontal component of its momentum at takeoff is  $[M\sqrt{(dg)}] \cos 45^\circ = M\sqrt{(dg/2)}$ . By the law of conservation of momentum, it gives equal momentum in the opposite direction to the tree trunk, thus point  $P$  on the trunk acquires velocity  $v$

$$v = (M/m)\sqrt{(dg/2)}. \quad (3.9)$$

Thus, the ape gives kinetic energy  $1/2(Mdg)$  to itself and kinetic energy  $1/2(M^2dg)/2m$  to the tree. The work required is the sum of these,

$$\text{Work for jump} = \frac{1}{2}Mdg[1 + (M/2m)]. \quad (3.10)$$

Table 1 shows that the energy costs of the observed manoeuvres were less than if the apes had jumped. Since the work required to sway the tree is proportional to its stiffness, it would be greater if the tree were thicker. The work required for a jump, however, is less for thicker trees with greater effective mass (equation (3.10)). Swaying is advantageous only if the tree is sufficiently slender which, in these cases, it was.

An animal that crossed a gap by descending to the ground and climbing up again to height  $h$  would have to do work  $Mgh$  against gravity alone. Table 1 shows that this would have been an order of magnitude greater than the energy required to sway the tree. It

appears that tree swaying was the most economical method for crossing this gap.

#### (b) Locomotion of wild orangutans

Orangutans mostly exhibit tree sway on supports that are less than 10 cm in diameter, and adult males may use tree sway as much as 10% of their travel time. But the use of compliant supports is not limited to this behaviour. Nearly 60% of orangutan locomotion relies exclusively on supports that are less than 10 cm in diameter and therefore likely to bend under their body weight. Observations of wild orangutans suggest that they actually use support compliance in many aspects of their locomotor behaviour. The following scenarios provide some examples of these behaviours and the benefits of support compliance.

- (i) An adolescent male, clinging to a liana angled at 45° to the vertical, wanted to enter the canopy of the next tree at a higher level than his current position. To do so, he grasped a lower terminal branch of a nearby tree, pulled himself down into the core of the tree and, in a catapult motion, launched himself up (while retaining hold of the angled liana) and managed to reach the desired terminal branch. Although the work returned in the recoil of the liana could not exceed the work done to stretch it when the male pulled himself into the adjacent tree, the liana acted like a catapult, recoiling in a shorter time than it was stretched. Consequently, the power was greater and added momentum to his movement.
- (ii) A mother, with her adolescent son close to her, tried to sway a tree trunk, but failed to produce oscillations of large enough magnitude to cross the gap. Her son moved to a higher bough in the tree, and she swayed the trunk again, this time to a great effect. The increased effective mass of the tree, due to the

son's higher position, may possibly have reduced the resonant frequency enough to enable the mother to power a greater amplitude of sway. Both mother and son crossed the gap, but on different levels.

- (iii) An adult male tree-swayed to cross a gap. When he had hold of a terminal branch in the tree he wished to enter, he maintained both footholds with the previous support and pulled himself along the branch into the core of the tree. Although he would have done work to pull himself into the tree, he was able to transfer onto a large and stiff bough, rather than losing height which must be regained by climbing, as would be the case if he had transferred onto a thin terminal branch.

This study seems to be the first to show that elastic compliance in branches and lianas can be used to reduce the energetic cost of gap crossing. Field observations suggest that this ability may be important in the locomotor ecology of a number of species, particularly orangutans. Further study of the dynamics between arboreal animals and compliant supports will help explain the diversity of locomotion and locomotor morphology in the primate order.

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