The extraordinary athletic performance of leaping gibbons

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The distance that animals leap depends on their take-off angle and velocity. The velocity is generated solely by mechanical work during the push-off phase of standing-start leaps. Gibbons are capable of exceptional leaping performance, crossing gaps in the forest canopy exceeding 10 m, yet possess none of the adaptations possessed by specialist leapers synonymous with maximizing mechanical work. To understand this impressive performance, we recorded leaps of the gibbons exceeding 3.7 m. Gibbons perform more mass-specific work (35.4 J kg⁻¹) than reported for any other species to date, accelerating to 8.3 ms⁻¹ in a single movement and redefining our estimates of work performance by animals. This energy (enough for a 3.5 m vertical leap) is 60 per cent higher than that achieved by galagos, which are renowned for their remarkable leaping performance. The gibbons’ unusual morphology facilitates a division of labour among the hind limbs, forelimbs and trunk, resulting in modest power requirements compared with more specialized leapers.

Keywords: leaping; work; power; primate; gibbon

1. INTRODUCTION

For any non-gliding animal, the distance of a leap depends on the direction and magnitude of its velocity vector at take-off. For a standing-start leap, the velocity achieved by the animal is limited by the amount of energy imparted to the body before take-off. This, in turn, is limited by the ability of the muscles to perform mechanical work on the body.

Specialized leapers demonstrate a number of adaptations that increase both the force applied to the substrate (e.g. the power-amplifying mechanisms of galagos [1], frog-hoppers [2], fleas [3] and locusts [4]), and the distance over which force is applied (e.g. the elongated distal leg segments of galagos [5] and frogs [6], the manipulation of the force-length characteristics of anuran leg muscle [7]). Adaptations such as these are synonymous with maximizing mechanical work and improving leap performance.

Behavioural strategies during the push-off and landing phases can significantly increase the mechanical work performed and lengthen the leap distance. Using a countermovement before the final push-off stretches the muscles and tendons of the hind limb, facilitating higher force production [8]. Similarly, swinging the forelimbs forward during take-off increases the forward displacement of the centre of mass, and hence, the push-off distance [9]. These behavioural strategies are widespread throughout the animal kingdom. Human athletes employ each of these strategies during high- and long-jump athletic events. Ancient Greek pentathletes even artificially added forelimb mass during standing jumps by employing halters, probably increasing jump distance by 5–7% [10].

Gibbons are lesser apes that inhabit the rainforests of Southeast Asia; they brachiate through the forest canopy but tend to leap across large gaps, preferring aerial leaps to ground level crossings because of the higher risk of predation by ground-dwelling carnivores. Field studies report that gaps in the canopy crossed by gibbons can exceed 10 m horizontally [11]. Leaping such long distances between trees high up in the forest canopy presents a major risk of a fall that could result in serious injury or death. Indeed, gibbon skeletons recovered from the forest floor display open fractures and other impact-related pathologies [12]. Therefore, the selective advantage of successful leaps is undoubtedly high [11,13].

Notwithstanding their exceptional leaping performance, gibbons display none of the anatomical adaptations usually associated with specialized leapers [14]. Exceptional muscle physiology (like that of the bonobo [14]) and/or behavioural strategies could, however, contribute to the remarkable leaping performance of the gibbons. Behavioural observations of the wild gibbons highlight the use of the forelimbs when leaping. The effectiveness of a forward armswing is probably more pronounced for gibbons compared with humans, because their forelimbs make up approximately 17 per cent of their body mass [15] compared with approximately 11 per cent in humans [16]. The goal of this study is to quantify the leap performance of the gibbons and to elucidate the biomechanical mechanisms behind performing long-distance leaps.

2. MATERIAL AND METHODS

Ten voluntary leaps by two captive white-handed gibbons (Hylobates lar, one adult male, one juvenile female) were recorded in high-definition videos (1920 × 1080 pixels, 25 frames per second, Sony HDR-SR1). The videos were de-interlaced yielding 50 fields per second using VIRTUALDUB (WWW.VIRTUALDUB.ORG). Measurements of the enclosure were taken using a laser measure (Bosch DLE-70) and a three-dimensional reconstruction of the island was created using trigonometry. The alignment of each branch with the plane of the camera (β) was calculated using a vertical calibration coefficient (CVERT = digitized vertical height of the trunk (in pixels)/the measured vertical height of the trunks in metres), the digitized length of each of the branches (Lb in pixels) and their respective measured lengths (bm in metres), such that:

\[ \beta = \cos^{-1}\left[\frac{L_{b}}{C_{VERT}}\right] \]

The gibbons centroid was found by drawing the gibbon’s outline in each video field manually using INKSCAPE (WWW.INKSCAPE.ORG). Each pixel of the resulting outline was given a weight of 1 and the centroid was found by resolving moments using custom-written software (LABVIEW 8.2, National Instruments, Austin, TX, USA), thus taking account of the gibbon’s limb movements when leaping. Video sequences were calibrated individually, using a vertical
Figure 1. (a) Body mass-specific power (black lines and symbols, primary y-axis) and work (red lines and symbols, secondary y-axis) versus log push-off distance for a range of species [1–4,17,18]. Dashed lines are logarithmic regressions. (Online version in colour.)

<table>
<thead>
<tr>
<th>Species</th>
<th>Body Mass-specific Power (W kg⁻¹)</th>
<th>Work (J kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Froghopper</td>
<td>4500</td>
<td>20</td>
</tr>
<tr>
<td>Human</td>
<td>3000</td>
<td>30</td>
</tr>
<tr>
<td>Gibbon</td>
<td>2500</td>
<td>40</td>
</tr>
<tr>
<td>Giraffe</td>
<td>2000</td>
<td>50</td>
</tr>
<tr>
<td>Elephant</td>
<td>1500</td>
<td>60</td>
</tr>
<tr>
<td>Lion</td>
<td>1000</td>
<td>70</td>
</tr>
<tr>
<td>Elephant</td>
<td>500</td>
<td>80</td>
</tr>
<tr>
<td>Human</td>
<td>250</td>
<td>90</td>
</tr>
<tr>
<td>Frog</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

Mean mass-specific power ($P_M$, in W kg⁻¹) and estimated force ($F_M$, in body weights, BW) were calculated as:

$$P_M = \frac{W_{\text{PUSH}}}{M},$$

and

$$F_M = \frac{U_R}{T_{\text{PUSH}}},$$

where the push-off time ($T_{\text{PUSH}}$) was defined as the stance phase duration of the take-off leg prior to take-off (frame error of 1/50 s or <9% stance phase duration, resulting in a maximum possible error of 7.8% and 8.7% in work and power, respectively), which could clearly be derived from the video recordings.

3. RESULTS

(a) Mechanical work

The maximum resultant distance leapt was 5.2 m; the highest take-off velocity was 8.3 ms⁻¹, requiring body mass-specific mechanical work of 34.5 J kg⁻¹. The 10 largest leaps recorded in 6 h of filming all exceeded 3.69 m in length, with mass-specific work surpassing 19 J kg⁻¹ (figure 1b). If 34.5 J kg⁻¹ of energy were directed vertically, then the resulting leap would be 3.5 m high (ignoring air resistance, which seems reasonable given Alexander’s estimates [19]). These values of mass-specific work comprehensively exceed those recorded for vertically leaping bonobos (11.3 J kg⁻¹; 1.2 m vertical displacement), humans (6.3 J kg⁻¹; 0.6 m [19]) and galagos (22 J kg⁻¹; 2.2 m; figure 1a) and represent the highest published values for any animal during a single movement. The wild gibbons reportedly leap up to 10 m [13], probably exceeding the values reported here for leaps greater than 3.69 m.

The gibbon leaps included a large countermovement and arm swing. The movements of the forelimb and trunk therefore contributed substantially to the work performed by the gibbon, lengthening the push-off distance to 1.04 m (figure 2). Thus, the distance over which work can be performed is equivalent to...
204 per cent of the anatomical hind limb length (i.e. the summed total of all the hind limb segments [14]). This far surpasses the relative push-off distances observed in other leaping primates; humans, 50 per cent; bonobo, 90 per cent [14]; moholi galago, 100 per cent [5] (figure 2). Taking muscle masses that probably contribute to these movements as a proportion of body mass (hind limbs, 11.9% [13]; forelimbs, 16% [17], back, 15%) yields a muscle mass-specific work of 81.9 J kg$^{-1}$ for the highest velocity leap in the gibbons. This is higher than theoretical estimates of maximal muscle mass-specific work of 70 J kg$^{-1}$ [20] but comparable with vertically leaping galagos (88 J kg$^{-1}$ [20]) and bonobos (92 J kg$^{-1}$ [17]).

(b) Mechanical power
The mean body mass-specific power achieved by the gibbons during the push-off of the highest velocity leap was 101.4 W kg$^{-1}$. This value is higher than that observed in bonobos (45 W kg$^{-1}$) and humans (27 W kg$^{-1}$ [1]), and substantially lower than that recorded for arthropod leapers (figure 1a; [2–4]). In muscle mass-specific terms, the gibbon’s power requirements (240 W kg$^{-1}$) are more modest than other primate leapers (bonobos, 615 W kg$^{-1}$ [17]; galagos, 800 W kg$^{-1}$ [1]), because of the contribution of the arms and trunk.

4. DISCUSSION
The magnitude of mass-specific mechanical work performed by the gibbons far exceeds recorded values for standing-start leaps by other taxa. Despite this, the power requirements are not extreme. Figure 1a indicates that, despite hind limb elongation, smaller leapers are limited to performing small amounts of work by their restricted ability to maintain contact with the substrate [8]. To compensate this, small leapers must store energy (work) in elastic mechanisms and release it over a very short time period [3]. This results in very high powers and forces equivalent to several hundred times BW [2]. Conversely, large animals are able to perform relatively more work because the body is accelerated over an absolutely longer distance and time period. The gibbon’s absolutely longer push-off distance (figure 2) produces lower powers and forces relative to their BW (the gibbons in this study, approx. 4 BW).

The mechanism used by the gibbons to perform the exceptional amount of mechanical work seen here is simple and is analogous to the use of halteres by Ancient Greek pentathletes [10]. The forward movement of the arms and the extension of the trunk during the push-off increases the distance over which force can be applied, i.e. the animal’s push-off distance. This action represents a division of labour among several body segments, the hind limbs, forelimbs and trunk. Thus, the massive forelimbs and flexible trunk, morphological adaptations undoubtedly associated with a suspensory lifestyle, find a crucial secondary adaptation during leaping.

A possible benefit to the gibbons of increasing work via this behavioural mechanism relates to their locomotor lifestyle. Specialist leapers adapted for producing high power possess highly specialized hind limbs, and consequently are confined to a predominantly saltatorial lifestyle. The gibbon’s large body mass, coupled with the compliance of the canopy substrates, precludes a saltatorial lifestyle. Instead, the gibbons maintain a morphology that allows them to employ a diverse locomotor repertoire to travel through the complex forest canopy [21]. Further, performing work while minimizing power probably avoids large branch deflections and hence energy losses when leaping.

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Figure 2. (a) Showing the gibbon’s posture throughout the push-off phase. Crossed circles indicate the centre of mass (CoM) position of the gibbon in the last four outlines; solid circles show CoM position for the frames between each outline. The double arrow-headed line indicates the distance the CoM moves before take-off. Black dashed lines indicate the position of the hindlimb, the adjoining arrow gives the sum of the segment lengths. (b) Anatomical leg lengths and vertical displacement of the centre of mass during standing-start leaps of moholi galago [1], bonobo, and humans [14] (left to right). (Online version in colour.)
The leap distances observed in this study were significantly lower than those observed in the wild gibbons. Without knowing the leap trajectories, it is impossible to know the biomechanical performance of the leaps of the wild gibbons. Yet, it seems feasible that for the longest ‘wild’ leaps, the observable muscle powers could reach those observed in the closely related bonobo, with a congruent increase in the work performed.

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