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A system for 2- and 3D kinematic and kinetic analysis of locomotion, and its application to analysis of the energetic efficiency of jumping locomotion

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With 2 figures and 1 table in the text

Summary: Kinematic analysis of film and video recordings is a standard technique in studies of the mechanics of locomotion. With the addition of segment mass data, kinematic analysis may be extended to estimate the forces, torques and bending loads imposed on limb segments, using inverse dynamic analysis. A software/hardware system for 2- and 3D kinematic and dynamic analysis is described, based on digitized images from multiple video cameras and featuring solid-rendered animations with true perspective. The capabilities of the system are described by reference to a study of jump take-off angles in 6 prosimian primates; and difficulties and limitations of this and similar techniques are reviewed.

Zusammenfassung: Die kinematische Analyse von Film- und Video-Aufzeichnungen ist eine Standard-Technik in Studien über die Mechanik der Lokomotion. Unter Heranziehung von Daten über die Segmentmassen können kinematische Analysen auf die Berechnung der Kräfte, Drehmomente und Biegebeanspruchungen der Segmente erweitert werden. Hierbei wird eine „inverse dynamische Analyse“ vorgenommen, d.h. der Untersuchungsgang geht von den beobachteten Bewegungen aus und ermittelt die inneren Kräfte, während die herkömmliche Mechanik die inneren Kräfte vorgibt und daraus die Bewegungen ableitet. Ein System aus Hardware und Software wird beschrieben, mit dem man 2- und 3-dimensionale kinematische und dynamische Analysen durchführen kann. Aus digitalisierten Einzelbildern mehrerer synchron laufender Videokameras werden die Daten gewonnen, aus denen man die Bewegungsabläufe auf dem Bildschirm simulieren kann in Gestalt von Körpern, die aus geometrischen Teil-Körpern zusammengesetzt sind. Die Möglichkeiten des Systems werden anhand einer Untersuchung über die Absprungwinkel bei 6 Arten von Prosimiern aufgezeigt. Schwierigkeiten und Grenzen der Anwendung werden umrissen.

Kinematic analysis

Kinematic analysis is the study of motion by consideration of the positions of all the components of a system with respect to time. Most modern motion studies attempt to obtain quantitative data, permitting the calculation of velocities, accelerations, and from these, forces: this is dynamics, kinetic analysis applied to bodies not in equilibrium. Dynamic analysis permits the calculation of the minimum muscle forces which would be necessary to produce a given motion. However, since muscles act in groups for any given action, and since the number of muscles and motor units present is considerably greater than the number required to control the mechanism (ALEXANDER 1983) it is impossible to identify the precise

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contribution of an individual muscle, even by simultaneous use of forceplate and electromyographic data (e.g. GÜNTHER 1989). Similarly, we can only determine the **minimum** level of forces acting at either end of any bone (ignoring the role of antagonists and synergists) and the **net** stress and strain thus induced in the bone, by these indirect methods.

Internal forces can, however, be measured directly, using strain gauges fixed to muscle tendons (e.g. RIEMERSA *et al.* 1988) for muscle force, or to bones (e.g. LANYON & BOURNE 1979), to measure the consequent bone strain. The latter data are particularly important, since the pattern of bone strain is known to have a fairly direct influence on bone shape, during the lifetime of individual animals, by stimulating remodelling (see, e.g. PAUWELS 1965, KUMMER 1972, CURREY 1984). However, it is difficult to record naturalistic activity using wired connections. Telemetry would permit the recording of more natural activity patterns, but here, size constraints imposed by current battery and signal multiplexing technology mean that at present this technique is practicable only for relatively large species (see, e.g. an excellent study of fruit bats by SWARTZ *et al.* (1992)). The results of such studies may be difficult to generalize, and invasive techniques are unacceptable for endangered species. It therefore seems likely that we will continue to rely primarily on dynamic analysis of external, non-invasive data to calculate internal forces, despite the limited resolution of this technique.

Recording techniques

Essentially, there are four alternative techniques for recording locomotor performances: high speed film, video, real-time automatic marker tracking, and use of angle/linear acceleration transducers. High speed film produces very high quality images, and framing rates of 500–10,000/second can be achieved. These figures are somewhat deceptive as the exposure time is usually a direct function of framing rate, and 1000/second rates may be required simply to freeze the motion. Film quality cannot be instantaneously checked however, timing accuracy may not be good, and synchronization of multiple cameras, for 3D work, remains a major problem. None of the latter problems apply to video, which also has the advantage of relatively low illumination requirements. However, standard (PAL, NTSC, etc.) video resolution (625 lines/frame, 312 lines/field) is not high and framing rates are limited to 50 (PAL) or 60 (NTSC) video fields/second. While HDTV promises improvement on resolution, the non-standard video used in high-speed video systems such as the Kodak Motion Analyser System, which operates at up to 1000 full frames/second, with the option of intensified imagers, is still very limited in resolution. It is videotape itself which is to a large extent the limiting factor. Hybrid video solutions, acquiring digitized video directly to computer memory, give approximately double the resolution of videotape: their storage time is currently relatively low (5 seconds or so at 1000 frames/second) but this limitation is not likely to endure.

Analysis of video or film records involves calibration of the optical system, and measurement of positions of interest on 200–1000 frames for each second of motion. Various computer-based automated marker-tracking systems have been developed to address this problem, such as VICOM, which can track 30 LED markers in three dimensions at frequencies up to 300 Hz. However, available systems are often prohibitively expensive, and their graphic displays limited to

stick-figure output, which is nearly unreadable in 3D. While, theoretically, the use of markers should greatly improve the accuracy of position data, mounting method is critical: direct bone mounting on experimental animals is extremely precise, but ethically dubious, and skin attachment over joints like the hip, more ethical but far less precise. Moreover, available LED markers are far too large to be attached to small animals. Being hardware-specific, in short, these systems are inflexible, and so are rarely found outside of clinical laboratories or sports-science institutions. Use of telemetered angle and acceleration transducers mounted externally is an intriguing alternative, which would avoid the major source of error in kinematic analysis, but the size/weight constraints which apply to telemetered strain-gauge studies also seem to have prevented implementation of this technique. There is, still, no ideal solution for motion analysis. All the above systems have their characteristic advantages and disadvantages.

In this paper, we report development of a flexible, low-cost, yet powerful system for 2- and 3-dimensional kinematic and kinetic analysis of locomotion. The system was applied to analysis of jumping locomotion in diurnal and nocturnal prosimian primates at Paris and Chester Zoos, where the high-speed Kodak Motion Analyzer System was used but animal activity unconstrained; and at Duke University Primate Center (DUPC) where animals were encouraged to jump between standard horizontal bar supports at controlled distances, using a food reward: here, standard PAL video was employed. Artificial lighting was limited to the minimum: intensifiers being used for the rarest species; red incandescent light for other nocturnals.

3D video recording

To record in 3D, two or (preferably) more cameras are arranged so that their fields of view cover the area to be filmed. In most video cameras, lens quality is sufficiently good to allow us to ignore optical distortion, and timing error is less than 1%. Framing rates can therefore be assumed accurate. The field of view is carefully chosen to be as small as possible, to maximize the resolution, and yet include all activity of interest. We found that it was not always possible to position two cameras to cover all four limbs at all times. Our system allows addition of more cameras, but this is not without its own problems.

All cameras must be precisely synchronized: this cannot yet be easily done using film cameras, but professional video-cameras and all video mixers have electronic synchronization via "genlocking". However, the more camera images are stored on a single recorder, using a video mixer, the smaller each image becomes.

While it is prohibitively expensive to duplicate the precision of calibration of still photogrammetric cameras, a variety of mathematical approximations allow adequate calibration of cameras in situ, e.g., the direct linear transform (DLT) equations (SHAPIRO 1978). Use of DLT does not, unlike most other photogrammetric approaches, require the optical axes of the cameras to be orthogonal, which is of great practical value, but in order to use DLT, the position of six or more known points must be recorded in the filming space. The more points recorded, and the more of the volume of interest they cover, the better (WOOD & MARSHAL 1986). Our reference object was a tripod-mounted 4×2 cm box with telescopic aerials on 5 faces, marked at regular distances, which were extended to fill the

maximum common field of view of the two cameras. However, when small, furry animals are the subject, the common field of view may be too small to permit acceptable definition of joint positions. Filming with orthogonally-arranged cameras at known distances does not require calibration of space, and would be the method of choice for small animals. The DLT approach is better reserved for larger species with more readily visible joints.

Video recordings, made on a portable VHS recorder, are transferred onto Hi-Band SP U-matic tape for editing and analysis. Video frames are made up of two sequential fields. Normal single frame advance on VHS equipment only displays even numbered fields, halving the temporal resolution. U-matic equipment allows access to all fields, but it is generally harder to get sufficiently good alignment for an interference free picture.

Perhaps the ideal tool for recording would be a read-write videodisk: these are currently moderately expensive, (approximately £ 10,000) but offer the benefit of immediate and accurate access to any location in the video sequence.

Digitization of joint positions

While measurements can be made directly from a monitor, the speed of localization is too slow to allow frames to be held frozen on the recorder while this is done. Therefore, using a digital framestore (framegrabber) we convert moving video, in real time, to digital images, 512 by 256 pixels, with 256 grey levels. Under software control, such devices can then split frames into individual fields, which can be displayed and measured on a computer monitor at leisure. Most framestores, however are incapable of continuous real-time conversion. While commercial animation controllers are available which overcome this problem, by locating time codes written on each field, these are very expensive. A much cheaper solution (SELLERS 1992) is based on a simplified modem circuit that converts signals transmitted from the computer port to audio tones which are then recorded onto the audio track of the videotape.

Kinematic analysis

Kinematic analysis requires that the positions of the joint centres are measured for each frame in a sequence. This measurement was performed using a Gait Analysis Program (GAP) developed by one of us (WIS), and at present implemented on Hewlett-Packard 9000 series graphics workstations. Image data acquired by the PC is passed to GAP via a local area network, and the software then allows the user to display the image on the computer screen, optionally enhanced and restored to the correct aspect ratio, and points are measured using the mouse driven pointer. Once a calibrated video sequence has been obtained, the program first requires measurement of a frame including the calibration object, which should define the origin of the coordinate system, and should have one other known point. Then a set of clearly visible points, related to skeletal landmarks, must be defined. Given the mechanical complexity of the mammalian body, a much simplified, "link segment" (BRESLER & FRANKEL 1950) model, is essential. This is input to the computer in the form of a data file for each set of experiments. The body is divided into a series of rigid links connected by unrestricted ball-and-socket "revolute" joints. GAP offers the option of displaying a measured series of

frames as an animated 3D model of the link system, where segments are displayed as smooth-shaded articulated solids with true perspective, rather than the stick figures familiar from commercial systems such as VICOM. Using a simple knob-box control system, the observer may zoom in on any part of the image, which may be fixed in space with respect to any node in the model, and rotate their viewpoint to any position around the model, which may be viewed at animation speeds up to real time. The visualization capability allows an immediate intuitive verification of the integrity of the model, and is a powerful tool in identification of errors in joint location. Each link can be considered in isolation, using the information known about its movement, to calculate the external forces acting upon it. These external forces must come from its contact with its surroundings, or, through its joints, from other links. In this way, the forces (both internal and external) necessary to produce the observed movement in the whole structure can be calculated. This procedure is known as inverse dynamic analysis, and has been implemented in GAP.

Signal processing

Because of the difficulty of accurately measuring joint centres, raw joint position data contains a random sampling error, in the form of high frequency noise. This becomes a problem during the process of differentiation needed to calculate the other kinematic parameters of velocity and acceleration, when the noise can be amplified to such an extent that the data becomes useless (WINTER 1990). Signal conditioning is thus essential. While the fitting of functions to the data is one means of providing smooth curves of velocities and acceleration, the resulting curves may owe more to the chosen function than the underlying mechanics of the filmed performance, so it is usually better to use a digital low-pass filter, which leaves appreciable noise, but is much more robust, and which more closely reflects the mechanics (PEZZACK et al. 1977).

Segment mass properties

In order to perform inverse dynamic analysis, the mass properties of the segments are required: length and mass of the segment; the relative position of the centre of mass along the segment; and the moment of inertia about the centre of mass. The moment of inertia is a measure of the distribution of the mass away from the centre of mass: it is the rotational analogue of mass. These values can be measured directly by sacrifice of the subject, but it has also been shown that resulting values vary very substantially from individual to individual (SMITH 1987). In humans, these values can be obtained by regression from published data, or by immersion (DEMPSTER 1961). LI (1991), however, has demonstrated that geometric approaches are an accurate, and far more flexible alternative, and a geometric approach supported by data in the prosimian literature (SMITH 1987, WELLS & DEMENTHON 1987) was adopted in this study. For most segments, segment centre of mass, and the relevant mass fraction could be obtained from the literature directly and the segment mass calculated from the measured total mass of the animal. However, when the segment definition was inappropriate, volumes were estimated from X-ray photographs and the mass fractions calculated accordingly. Segment lengths are of course available from the kinematic analysis data. To

calculate the moments of inertia for each segment, a purely geometric approach can be used. Each segment of the body is treated as a conic section with appropriate dimensions to fit the mass, length and centre of mass position criteria. The volume of each conic section is calculated from its mass and a mean figure for body density (APKARIAN et al. 1989). The calculated mass distribution data is summarized in Table 1.

Table 1. Mass distribution data.

		<i>M. murinus</i>	<i>L. catta</i>	<i>C. major</i>	<i>M. coquereli</i>	<i>G. garnettii</i>	<i>G. moholi</i>
Lower arm	Mass (kg)	$3.13 \cdot 10^{-3}$	$1.35 \cdot 10^{-1}$	$1.70 \cdot 10^{-2}$	$1.75 \cdot 10^{-2}$	$5.63 \cdot 10^{-2}$	$9.24 \cdot 10^{-3}$
	CM	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$
	MOI (kg.m ²)	$2.35 \cdot 10^{-7}$	$1.27 \cdot 10^{-4}$	$2.70 \cdot 10^{-6}$	$3.69 \cdot 10^{-6}$	$3.60 \cdot 10^{-5}$	$1.22 \cdot 10^{-6}$
Upper arm	Mass (kg)	$2.88 \cdot 10^{-3}$	$1.24 \cdot 10^{-1}$	$1.56 \cdot 10^{-2}$	$1.61 \cdot 10^{-2}$	$5.40 \cdot 10^{-2}$	$6.72 \cdot 10^{-3}$
	CM	$5.18 \cdot 10^{-1}$	$5.18 \cdot 10^{-1}$	$5.18 \cdot 10^{-1}$	$5.18 \cdot 10^{-1}$	$4.66 \cdot 10^{-1}$	$4.66 \cdot 10^{-1}$
	MOI (kg.m ²)	$1.77 \cdot 10^{-7}$	$1.15 \cdot 10^{-4}$	$2.46 \cdot 10^{-6}$	$3.09 \cdot 10^{-6}$	$2.37 \cdot 10^{-5}$	$8.35 \cdot 10^{-7}$
Fore-foot	Mass (kg)	$8.75 \cdot 10^{-4}$	$3.78 \cdot 10^{-2}$	$4.76 \cdot 10^{-3}$	$4.90 \cdot 10^{-3}$	$2.25 \cdot 10^{-2}$	$4.20 \cdot 10^{-3}$
	CM	$5.73 \cdot 10^{-1}$	$5.73 \cdot 10^{-1}$	$5.73 \cdot 10^{-1}$	$5.73 \cdot 10^{-1}$	$5.73 \cdot 10^{-1}$	$5.73 \cdot 10^{-1}$
	MOI (kg.m ²)	$1.26 \cdot 10^{-8}$	$5.14 \cdot 10^{-6}$	$1.96 \cdot 10^{-7}$	$2.18 \cdot 10^{-7}$	$1.97 \cdot 10^{-6}$	$2.07 \cdot 10^{-7}$
Hind-foot	Mass (kg)	$8.75 \cdot 10^{-4}$	$3.78 \cdot 10^{-2}$	$4.76 \cdot 10^{-3}$	$4.90 \cdot 10^{-3}$	$1.13 \cdot 10^{-2}$	$2.52 \cdot 10^{-3}$
	CM	$4.78 \cdot 10^{-1}$	$4.78 \cdot 10^{-1}$	$4.78 \cdot 10^{-1}$	$4.78 \cdot 10^{-1}$	$4.78 \cdot 10^{-1}$	$4.78 \cdot 10^{-1}$
	MOI (kg.m ²)	$1.32 \cdot 10^{-8}$	$4.94 \cdot 10^{-6}$	$2.17 \cdot 10^{-7}$	$2.26 \cdot 10^{-7}$	$1.41 \cdot 10^{-6}$	$1.35 \cdot 10^{-7}$
Calf	Mass (kg)	$3.38 \cdot 10^{-3}$	$1.46 \cdot 10^{-1}$	$1.83 \cdot 10^{-2}$	$1.89 \cdot 10^{-2}$	$6.08 \cdot 10^{-2}$	$1.39 \cdot 10^{-2}$
	CM	$4.01 \cdot 10^{-1}$	$4.01 \cdot 10^{-1}$	$4.01 \cdot 10^{-1}$	$4.01 \cdot 10^{-1}$	$6.08 \cdot 10^{-1}$	$6.08 \cdot 10^{-1}$
	MOI (kg.m ²)	$3.57 \cdot 10^{-7}$	$1.61 \cdot 10^{-4}$	$6.86 \cdot 10^{-6}$	$5.39 \cdot 10^{-6}$	$4.08 \cdot 10^{-5}$	$4.15 \cdot 10^{-6}$
Thigh	Mass (kg)	$1.03 \cdot 10^{-2}$	$4.43 \cdot 10^{-1}$	$5.57 \cdot 10^{-2}$	$5.74 \cdot 10^{-2}$	$1.37 \cdot 10^{-1}$	$4.20 \cdot 10^{-2}$
	CM	$4.47 \cdot 10^{-1}$	$4.47 \cdot 10^{-1}$	$4.47 \cdot 10^{-1}$	$4.47 \cdot 10^{-1}$	$5.61 \cdot 10^{-1}$	$5.61 \cdot 10^{-1}$
	MOI (kg.m ²)	$1.26 \cdot 10^{-6}$	$7.39 \cdot 10^{-4}$	$2.46 \cdot 10^{-5}$	$2.83 \cdot 10^{-5}$	$1.48 \cdot 10^{-4}$	$1.73 \cdot 10^{-5}$
Head	Mass (kg)	$6.38 \cdot 10^{-3}$	$2.75 \cdot 10^{-1}$	$3.46 \cdot 10^{-2}$	$3.57 \cdot 10^{-2}$	$1.20 \cdot 10^{-1}$	$2.08 \cdot 10^{-2}$
	CM	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$
	MOI (kg.m ²)	$7.30 \cdot 10^{-7}$	$2.88 \cdot 10^{-4}$	$1.16 \cdot 10^{-5}$	$1.17 \cdot 10^{-5}$	$7.92 \cdot 10^{-5}$	$3.37 \cdot 10^{-6}$
Torso	Mass (kg)	$3.26 \cdot 10^{-2}$	$1.41 \cdot 10^{+0}$	$1.77 \cdot 10^{-1}$	$1.82 \cdot 10^{-1}$	$6.15 \cdot 10^{-1}$	$1.05 \cdot 10^{-1}$
	CM	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$	$5.00 \cdot 10^{-1}$
	MOI (kg.m ²)	$1.82 \cdot 10^{-5}$	$9.58 \cdot 10^{-3}$	$3.05 \cdot 10^{-4}$	$3.06 \cdot 10^{-4}$	$1.94 \cdot 10^{-3}$	$1.12 \cdot 10^{-4}$
Tail	Mass (kg)	$2.19 \cdot 10^{-3}$	$9.45 \cdot 10^{-2}$	$1.19 \cdot 10^{-2}$	$1.23 \cdot 10^{-2}$	$4.84 \cdot 10^{-2}$	$5.25 \cdot 10^{-3}$
	CM	$3.78 \cdot 10^{-1}$	$3.78 \cdot 10^{-1}$	$3.78 \cdot 10^{-1}$	$3.78 \cdot 10^{-1}$	$3.78 \cdot 10^{-1}$	$3.78 \cdot 10^{-1}$
	MOI (kg.m ²)	$2.33 \cdot 10^{-6}$	$1.13 \cdot 10^{-3}$	$4.57 \cdot 10^{-5}$	$5.39 \cdot 10^{-5}$	$1.11 \cdot 10^{-4}$	$1.06 \cdot 10^{-5}$

Trajectory

In addition to the individual segment centres of mass, the overall model has a centre of mass that can be calculated from the positions of the individual centres of mass. Once the overall centre of mass has been calculated for each frame of the film, then the trajectory of the animal (the path followed by the centre of mass) can be produced. This can be plotted out and the initial gradient calculated, giving the takeoff angle for the animal. In practice, the takeoff angle was calculated by fitting a straight line to the centre of mass position between the start of the jump (position of maximum flexion) to toe-off and calculating the gradient of this line.

Inverse dynamics

The link segment model, and the output of the kinematic analysis module of GAP, together with information on segment mass and inertial properties, can be passed directly to the inverse dynamic analysis module. Forces are calculated by analyzing reactions and accelerations operating on each limb segment, considered as an isolated unit. The program works sequentially, from the free end of a distal segment, moving first proximally, and then out to distal segments, if an external reaction force is to be estimated. Such external reaction forces can be verified if force plate data are available. GAP will calculate angular accelerations, forces across joints and resultant muscle torques. The techniques used are those detailed in WINTER (1990). Since we do not know of any satisfactory non-contact technique for accurate measurement of rotations of segments about their axes, this element of a full 3D kinetic analysis is not included in GAP. Inverse dynamic analysis depends on an accurate knowledge of accelerations, and is therefore very vulnerable to noise arising from measurement error. Where this is likely to be a problem, predictive mechanical modelling using artificial datasets (SELLERS 1992 and in prep.) can permit verification of the model.

A study of jump takeoff angles

Using this system, we have investigated the mechanics of jumping in 6 prosimian primates, and we summarize here some of our early findings on takeoff trajectories, in order to illustrate its possible applications. We concentrate on the question of whether saltatory species optimize their energy consumption during jumping (other aspects of the mechanics of prosimian leaping are considered e.g., in PETERS & PREUSCHOF 1985 and GÜNTHER et al. 1991).

When jumping a gap of a particular size, an animal can control two important physical parameters of the jump: its takeoff velocity and its angle of trajectory. An animal can minimize its takeoff velocity by choosing a takeoff angle of 45°, or by selecting a shallower or a steeper trajectory, which implies a higher takeoff velocity. What are the costs and benefits of the alternative options?

The mechanical energy cost is simply the kinetic energy of the animal at takeoff:

$$E_{KE} = \frac{mrg}{2\sin 2\Theta} \quad (1)$$

Where E_{KE} is the kinetic energy of the animal at takeoff, m its mass, r the range of the jump, g the acceleration due to gravity and Θ the takeoff angle. The equation is shown graphically in Fig. 1.

From Fig. 1, it can be seen that the most economical takeoff angle (the one that leads to the longest jump for the least energy expenditure) is 45°, and one would expect that this is the takeoff angle that would be chosen by the animal. Five species, *Cheirogaleus major*, *Galago garnettii*, *Galago moholi*, *Microcebus murinus* and *Mirza coquereli* were filmed jumping a series of increasing distances under standardized conditions at DUPC, and one (*Lemur catta*) filmed jumping a single distance at Chester Zoo. The jumps were analyzed using GAP, and are displayed in Fig. 2.

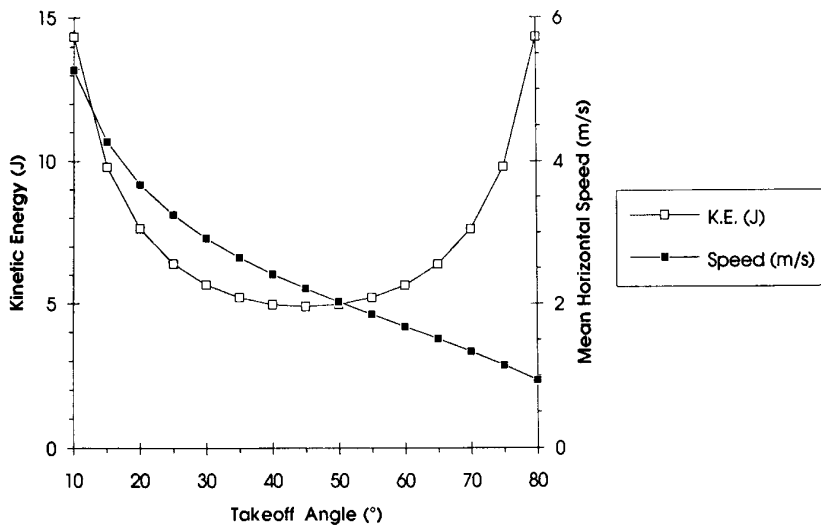


Fig. 1. Graph showing the relationship between the takeoff angle and kinetic energy cost, and takeoff angle and horizontal velocity for an animal jumping 1 m.

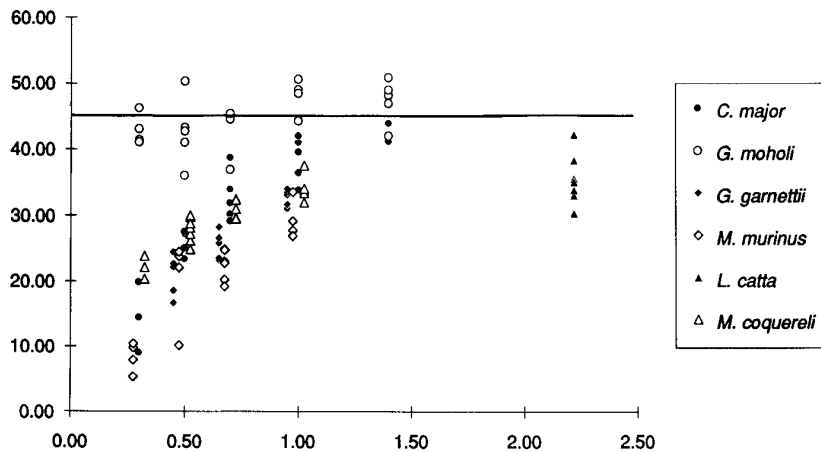


Fig. 2. Graph showing observed takeoff angles for various jump distances in *Cheirogaleus major*, *Galago garnettii*, *Galago moholi*, *Microcebus murinus* and *Mirza coquereli* and for one distance in *Lemur catta*.

It is immediately apparent that, except for *Galago moholi*, these animals do **not** usually jump at the energetically optimal angle of 45°. They jump at appreciably shallower angles. However, as the jump distance increases, they all do jump at more energetically efficient angles and it would certainly be expected that they would jump at 45° for their longest jumps. Thus, excepting *G. moholi*, only *Cheirogaleus major*, the least frequent jumper of the group, achieved a 45° takeoff angle in our study. It is probable that 1.4 m, the longest jump recorded, is near its maximum jumping distance and it is therefore hardly surprising that at this distance *C. major* does use the optimal jump trajectory. Since these animals do not habitually jump at the energetically most efficient angle, then there must be other significant benefits associated with shallower and less efficient trajectories. One reason could be that the animals are prepared to trade-off some loss in energetic efficiency for a gain in travelling speed. The horizontal speed of a jump is given by:

$$V_h = v_{to} \cos\theta \quad (2)$$

Where V_h is the horizontal velocity and V_{to} the takeoff velocity. Thus the relationship between speed and jump angle can be calculated:

$$v_h = \cos\theta \sqrt{\frac{rg}{\sin 2\theta}} \quad (3)$$

This relationship is shown graphically, against kinetic energy cost, in Fig. 1. It is clear from this graph that lower trajectories give faster jump speeds, and lower travel times. A time-pressured animal thus has to decide on a compromise between the relatively high cost of a very quick jump and the relative slowness of an energetically efficient one. On longer jumps, the range of choice in jump angle is more restricted because the minimum takeoff velocity for the jump is a larger fraction of the maximum takeoff velocity that the animal can manage and it therefore has less scope for selecting a faster, flatter trajectory. "Ecological" benefits: faster travel between well-spaced food patches, reduction in vulnerability to avian predators, and (perhaps) better ability to move through dense-packed vegetation may be more important than energy-efficiency. It is salutary to discover that a formal biomechanical analysis of locomotor behaviour may produce, as here, results of considerable relevance to understanding of prosimian ecology. Such an ability to feed back directly into behavioural field studies amply justifies development of this kinematic analysis system.

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References

- ALEXANDER, R. MCN. (1983): Animal mechanics. – Blackwell Scientific, Oxford.
 APKARIAN, J., NAUMANN, S. & CAIRNS, B. (1989): A three dimensional kinematic and dynamic model of the lower limb. – J. Biomechanics 22, 143–155.

- BRESLER, B., FRANKEL, J.P. (1950): The forces and moments in the leg during level walking. – Trans. ASME. **72**, 27–36.
- CURREY, J.D. (1984): The Mechanical Adaptations of Bones. – Princeton University Press, Princeton NJ.
- DEMPSTER, W. (1961): Free-body diagrams as an approach to the mechanics of human posture and motion. – In: GAYNOR, F. (ed.): Biomechanical Studies of the Musculo-Skeletal System. – Charles C. Thomas Publisher, Springfield, Illinois, pp. 81–135.
- GÜNTHER, M.M. (1989): Funktionsmorphologische Untersuchungen zum Sprungverhalten an mehreren Halbaffenarten (*Galago moholi*, *Galago (Otolemur) garnettii*, *Lemur catta*). – PhD. Thesis, Freie Universität Berlin.
- GÜNTHER, M.M., ISHIDA, H., KAMAKURA, H. & NAKANO, Y. (1991): The jump as a fast mode of locomotion in arboreal and terrestrial biotopes. – Z. Morph. Anthropol. **78**, 341–372.
- KLEPPNER, D. & KOLENKOW, R.J. (1973): An introduction to mechanics. – McGraw-Hill, London.
- KUMMER, B.K.F. (1972): Biomechanics of Bone: mechanical Properties, Functional Structure, Functional Adaptation. – In: FUNG, Y. C., PERRONE, N. & ANLIKER, M. (eds.): Biomechanics – Its Foundations and Objectives. – Prentice-Hall, Englewood Cliffs.
- LANYON, L. E. & BOURNE, S. (1979): The influence of mechanical function on the development and remodelling of the tibia. An experimental study in sheep. – J. Bone Jt. Surg. **61A**, 263–273.
- LI, Y. (1991): Ontogeny of children's limbs – with particular reference to inertial characteristics. – PhD. Thesis, University of Liverpool.
- PAUWELS, F. (1965): Gesammelte Abhandlungen zur funktionellen Anatomie des Bewegungsapparates. – Springer, Berlin.
- PETERS, A. & PREUSCHOTT, H. (1984): External biomechanics of leaping in *Tarsius* and its morphological and kinematic consequences. – In: NIEMITZ, C. (ed.): Biology of Tarsiers. – Gustav Fischer, Stuttgart, pp. 227–255.
- PEZZACK, J. C., NORMAN, R.W. & WINTER, D. A. (1977): An assessment of derivative determining techniques used for motion analysis. – J. Biomech. **10**, 377–382.
- RIEMERSA, D. J., VAN DEN BOGART, A. J., SCHAMHARDT, H. C. & HARTMAN, W. (1988): Kinetics and kinematics of the equine hind limb: in vivo tendon strain and joint kinematics. – Amer. J. Vet. Res. **49**, 1353–1359.
- SELLERS, W.S. (1992): A Study of the Mechanics of Leaping in Prosimian Primates. – PhD. Thesis, University of Liverpool.
- SHAPIRO, R. (1978): Direct linear transformation method for three-dimensional cinematography. – Research Quarterly **49**, 197–205.
- SMITH, R.M. (1987): Biomechanics of the locomotion of *Galago senegalensis*. – Arizona State University, Arizona.
- SWARTZ, S., BENNETT, M. B. & CARRIER, D.R. (1992): Wing bone stresses in free flying bats and the evolution of skeletal design for flight. – Nature **359**, 726–729.
- WELLS, J. P. & DEMENTHON, D. F. (1987): Measurement of body segment mass, center of gravity, and determination of moments of inertia by double pendulum in *Lemur fulvus*. – Amer. J. Primatol. **12**, 299–308.
- WINTER, D.A. (1990): Biomechanics and motor control of human movement. – John Wiley & Sons, New York.
- WOOD, G. A. & MARSHAL, R. N. (1986): The accuracy of DLT extrapolation in three-dimensional film analysis. – J. Biomech. **19**, 781–785.

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