

Effects of limb mass distribution on mechanical power outputs during quadrupedalism

David A. Raichlen

Department of Anthropology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138, USA

e-mail: raichlen@fas.harvard.edu

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Summary

Many researchers have suggested that cursorial mammals concentrate limb muscle mass proximally to reduce energy costs during locomotion. Although supported by experiments where mass is added to an individual's limbs, mammals with naturally occurring distally heavy limbs such as primates have similar energy costs compared with other mammals. This study presents a new hypothesis to explain how animals with distally heavy limbs maintain low energy costs. Since distal mass should increase energy costs due to higher amounts of muscular power outputs, this hypothesis is based on the divergent effects of stride frequency on internal and external power outputs (the power output to move the limbs and the body center of mass, respectively). The use of low stride frequencies reduces limb velocities and therefore decreases internal power, while associated long strides increase the vertical displacement of the body center of mass and therefore increase external power. Total power (the sum of internal and external power) may therefore not differ among mammals with different limb mass distributions. To test this hypothesis, I examined a sample of infant baboons (*Papio cynocephalus*) during ontogeny and compared them with more cursorial

mammals. Limb mass distribution changes with age (from distal to more proximally concentrated) in baboons, and the infants used shorter strides and higher stride frequencies when limb mass was most proximally concentrated. Compared with non-primates who have more proximally concentrated limb mass, the infants used longer strides and lower stride frequencies. Relatively low internal power was associated with low stride frequencies in both the intra- and inter-specific samples. However, only in the inter-specific comparison were relatively long strides associated with high external power outputs. In both the intra-specific and the inter-specific samples, total power did not differ between groups who differed in limb mass distribution. The results of this study suggest that a trade-off mechanism is available to quadrupeds with distally heavy limbs allowing them to maintain similar total power outputs (and likely similar energy costs) compared with mammals with more proximally concentrated limb mass.

Key words: biomechanics, primate, locomotion, inertial properties, baboon, *Papio cynocephalus*.

Introduction

Reducing the energy costs of locomotion may be an important consideration in mammalian limb design (see Hildebrand, 1985; Hildebrand and Hurley, 1985; Myers and Steudel, 1985; Steudel, 1990). For example, cursorial mammals tend to concentrate limb mass proximally, leaving their distal limb elements slender and light (Hildebrand, 1985; Lieberman et al., 2003). Theoretically, distally heavy limbs should increase energetic costs due to increases in internal power – the amount of muscular power (the rate that muscles do work) required to move limb segments relative to the body (see Hildebrand and Hurley, 1985; Dellanini et al., 2003). Although the relationship between power outputs and energy costs of locomotion remains unclear (see Heglund et al., 1982a; Kram and Taylor, 1990; Minetti et al., 1999), recent studies

suggest that the cost of swinging the limbs may comprise up to 25% of the cost of locomotion (Marsh et al., 2004; Modica and Kram, 2005; Pontzer et al., 2005). Despite the possible energetic constraints on limb design, several mammals, such as primates, have evolved distally heavy limbs (Preuschoft and Günther, 1994; Raichlen, 2004). This study examines locomotor ontogeny in infant baboons to determine how ontogenetic changes in limb mass distribution impact power outputs.

Experimental studies have generally confirmed that higher costs are associated with distal limb loading (Myers and Steudel, 1985; Steudel, 1990). However, in the only comparative experimental study of the energetic cost of naturally occurring distal limb mass, Taylor et al. (1974) showed that three mammals who differed greatly in their limb

mass distributions (cheetah, gazelle and goat) did not differ significantly in their energetic costs of locomotion at a given velocity. Quadrupedal primates offer another example that confounds predicted higher costs due to heavy distal limb elements (Taylor et al., 1982; Heglund, 1985; Steudel-Numbers, 2003). Primates have distally heavy limb muscles that control grasping hands and feet, yet their energetic costs do not differ from those of similarly sized mammals (Taylor et al., 1982; Heglund, 1985; Steudel-Numbers, 2003). Although the results of Taylor et al. (1974) have been called into question because of methodological concerns (see Lieberman et al., 2003), their study, combined with the primate data, suggests that limb mass distributions do not necessarily determine energy costs.

The purpose of the present study is to explore mechanisms used by quadrupeds with distally heavy limbs that allow them to maintain similar energy costs compared with mammals with more proximal limb mass concentrations. Without a mechanism, the evolution of distally heavy limbs could have come with a great energetic price. Any mechanism must begin by reducing the impacts of limb mass distribution on internal power. The total power output during quadrupedalism is, however, generally divided into two parts: external power is the power required to lift and accelerate the body center of mass, and internal power is the power required to move the limbs relative to the body center of mass (Heglund et al., 1982b; Minetti et al., 1999). Taxa with distally heavy limbs must find a way to minimize the impacts of their limb mass on internal power and therefore maintain similar total power outputs compared to mammals with more proximally concentrated limb mass.

Adjustments in kinematics may represent a mechanism that could mitigate the added energy costs of distally heavy limbs, since locomotor kinematics can have a strong impact on power outputs during locomotion (Hildebrand and Hurley, 1985; Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). For example, several researchers have shown that a change in stride frequency at a given velocity has divergent effects on internal and external power (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). Relatively low stride frequencies reduce the velocity at which muscles and tendons must move a limb, thereby reducing internal power (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). Relatively low stride frequencies are associated with relatively long strides (since velocity is the product of stride frequency and stride length), and long strides increase external power due to larger vertical displacements of the body center of mass (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). Interestingly, although humans walk and run with stride frequencies that nearly minimize total power, they deviate slightly from optimum stride frequencies (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995).

Although freely chosen stride frequencies do not completely minimize total power, metabolic energy expenditure is minimized at freely chosen stride frequencies (Zarrugh and Radcliffe, 1978). There may be other constraints on stride frequency that allow individuals to minimize energy expenditure despite slightly higher power outputs. Humans' freely chosen stride frequencies closely match those predicted by the Force Driven Harmonic Oscillator model (FDHO) described by Holt et al. (1990). The FDHO models the lower limb as a harmonic oscillator whose period is dependent on limb inertial properties, but the limb also requires a periodic driving function (muscle activity) to maintain its oscillation amplitude (Holt et al., 1990; Holt et al., 1991). Freely chosen combinations of stride frequencies and lengths are well predicted by the FDHO, suggesting an optimal combination of kinematics that is related to limb mass distribution. Any deviations from the freely chosen frequency, either above or below, result in increased energy expenditure due to increased muscle activity (Holt et al., 1991). It is likely then, that stride frequencies are constrained by limb inertial properties so that a frequency is chosen to minimize the driving function (Holt et al., 1991).

This same tuning of kinematics to inertial properties may apply to quadrupeds as well. Stride lengths and stride frequencies appear to vary in a predictable way with differences in limb mass distribution (Raichlen, 2004; Raichlen, 2005a). Taxa with distally heavier limbs tend to walk with lower stride frequencies and longer strides (Preuschoft and Günther, 1994; Myers and Steudel, 1997; Raichlen, 2004; Raichlen, 2005a), and this trend appears valid both across mammalian taxa (Preuschoft and Günther, 1994; Myers and Steudel, 1997) and within ontogenetic samples where limb mass distributions change with age (Raichlen, 2005a). Additionally, lower stride frequencies are brought about by a combination of longer swing durations *and* longer stance durations. Thus, quadrupeds with distally heavy limbs could take advantage of the trade-offs between kinematics and power outputs simply by virtue of the fact that their stride frequencies are tuned to their limb inertial properties following the FDHO model. As a by-product of this tuning, kinematics may mitigate the energetic consequences of distally heavy limbs. If true then, compared with more cursorial taxa, quadrupeds with distally heavy limbs using lower stride frequencies would reduce internal power outputs (due to slower limb velocities during both swing and stance phase), while their longer strides would increase external power outputs so that total power outputs would not differ among individuals regardless of limb mass distribution.

Hypothesis testing

This study tests the hypothesis that quadrupedal kinematics associated with distally heavy limbs allows individuals to benefit from the trade-off mechanism described above and, therefore, they can maintain similar total power outputs compared with quadrupeds with distally lighter limbs. Two samples are used to test this hypothesis. First, a sample of

infant baboons (*Papio cynocephalus*) was examined during development. Primate ontogeny offers a natural experiment because infant primate limb mass distributions change with age (Grand, 1977; Turnquist and Wells, 1994; Raichlen, 2005b). At young ages, infant primates have distally heavy limb muscles, used for strong grasping of their mothers fur, and limb mass becomes more proximally concentrated with age (Turnquist and Wells, 1994; Raichlen, 2005b). As they age, and mass becomes more proximally concentrated, the infant baboons use relatively higher stride frequencies and shorter strides (Raichlen, 2005a). Therefore, power outputs can be examined in this sample as both limb mass distributions and kinematics change. In the second test of the trade-off mechanism, infant baboons are compared with a sample of non-primate cursorial quadrupeds who have more proximal limb mass concentrations. This sample of infant baboons uses lower stride frequencies and longer strides than other mammals (Raichlen, 2005a) and therefore may use these kinematic differences to maintain similar total power outputs compared with other mammals.

Hypothesis 1. Infant baboons with distally heavy limbs (younger individuals) should have lower internal and higher external power compared with older individuals because of their lower stride frequencies and longer strides. However, age-related differences in internal and external power should lead to similar total power at all ages.

Hypothesis 2. Because of their more distally heavy limbs compared with non-primates, the infant baboons use lower stride frequencies and longer strides than more cursorial non-primates (Raichlen, 2005a). Due to these kinematic differences, internal power should be lower, external power should be higher, and total power should not differ significantly between the baboons and the non-primates.

Materials and methods

Sample

Three infant baboons (*Papio cynocephalus* Linnaeus 1758; two females and one male; Table 1) were obtained from the Southwest Foundation for Biomedical Research (SFBR, San Antonio, TX, USA) from a population rejected by their mothers and placed in the SFBR nursery. Infant baboons were housed at the University of Texas Animal Resource Center using methods approved by both the University of Texas Institutional Animal Care and Use Committee (IACUC) and the SFBR IACUC. The study period lasted for approximately nine months, corresponding to the time during which the infants could be handled safely without administering anesthesia.

Inertial properties

Body segment inertial properties of the infant baboons were calculated using a geometric modeling technique (Raichlen, 2004; Raichlen, 2005b). Briefly, each body segment was modeled as a column with a circular cross section. Model shapes were constructed using external circumference

Table 1. Description of sample and number of strides analyzed at each age

| Subject | Age (months) | <i>n</i> |
|------------------|--------------|----------|
| Infant 1 (17194) | 3.33 | 9 |
| | 4.27 | 10 |
| | 4.73 | 10 |
| | 5.87 | 16 |
| | 6.10 | 32 |
| | 7.50 | 26 |
| Infant 2 (18573) | <3.0 | 21 |
| | 3.67 | 19 |
| | 4.67 | 38 |
| | 4.97 | 31 |
| | 5.53 | 18 |
| | 7.40 | 13 |
| | 8.10 | 22 |
| Infant 3 (18572) | <4.7 | 5 |
| | 4.70 | 20 |
| | 5.00 | 11 |
| | 5.57 | 12 |
| | 6.23 | 23 |
| | 7.43 | 33 |
| | 8.13 | 29 |
| | 8.97 | 69 |

Subject describes the infant number that is used in the text; the SFBR identification number is listed in parentheses. Infant 1 is male; infants 2 and 3 are female. *n* is the number of accepted strides analyzed and is included here for each sampled age.

measurements taken at three locations on each limb segment. From these measurements, column models were constructed, and segment inertial properties (mass, center of mass, mass moments of inertia) were calculated (Raichlen, 2004; Raichlen, 2005b). The natural pendular period (*NPP*) of the limbs was also calculated. The *NPP* is the duration of one complete oscillation of the limb if it was swinging as a pure pendulum and is calculated according to the following equation:

$$NPP = 2\pi \sqrt{\frac{I}{Mg(D)}}, \quad (1)$$

where *I* is the limb's mass moment of inertia about the proximal joint (the shoulder in the forelimb or the hip in the hindlimb), *M* is the limb's mass, *g* is acceleration due to gravitational forces (9.8 m s⁻²) and *D* is the distance of the center of mass from the proximal joint. The *NPP* represents an important link between limb mass distribution and kinematics because swing phase is often modeled as an approximation of a pendulum (see Mochon and McMahon, 1980; Mochon and McMahon, 1981; Holt et al., 1990; Holt et al., 1991). Larger *NPP*s due to more distal limb mass imply longer swing durations and therefore longer stride durations. Raichlen (2005a) has also shown that relatively large *NPP*s lead to relatively long stance durations. The use of *NPP* in this study

is not meant to imply that swing phase is purely passive, with no muscular action involved (see Marsh et al., 2004; Modica and Kram, 2005), but that limb motion during swing phase is tuned to the *NPP* (see Holt et al., 1990; Holt et al., 1991). *NPPs* were made dimensionless (*dNPP*) (according to Hof, 1996) to compare values among individuals who differed in body size and therefore limb length (*h*):

$$dNPP = \frac{NPP}{\sqrt{\frac{h}{g}}} \quad (2)$$

Grouping

Individuals were grouped based on their limb inertial properties, and these groupings did not conform to arbitrary age classes. Specifically, changes in *dNPP* were used to group infants according to limb mass distributions. Researchers have shown that limb *NPPs* change during swing phase due to flexion and extension of limb joints and that this change should be taken into account when comparing the effects of inertial properties on locomotion (Myers and Steudel, 1997; Raichlen, 2004; Raichlen, 2005a). When swing-phase inertial properties are compared [by calculating the minimum *dNPP* during swing phase (*dNPP_{min}*)], the infant baboons do not show a gradual change with age (Raichlen, 2005a). In fact, each individual falls into two groups: Group 1 comprises the young infants with distally heavy limbs and *dNPP_{min}s* that do not differ significantly, and Group 2 comprises older infants who have more proximal concentrations of limb mass and *dNPP_{min}s* that do not differ significantly (Raichlen, 2005a). Between the two groups, *dNPP_{min}s* do differ significantly (Raichlen, 2005a). These groupings proved robust in an examination of the effects of inertial properties on kinematics, with Group 1 infant baboons (more distal limb mass) using relatively lower stride frequencies and longer strides than Group 2 infants (Raichlen, 2005a).

Mechanical power

Three-dimensional kinematic data were obtained from each infant baboon at regular intervals during development (Table 1). Infant baboons were allowed to walk and run at freely chosen velocities through a Lexan tunnel made up of three removable sections (0.61 × 0.91 × 1.22 m each). Prior to tunnel entry, spherical reflective markers (14 mm; Oxford Metrics Inc., Oxford, UK) were glued to the major joints of the forelimbs and hindlimbs of each infant baboon (hip, knee, ankle, shoulder, elbow, knee). The placement of each marker was consistent with the segment definitions used for inertial property data collection (see Raichlen, 2005b).

Three-dimensional marker trajectories were captured for one side of the body during each locomotor trial using a five-camera 60 Hz Vicon 250 data acquisition system (Oxford Metrics Inc.). In addition to the Vicon system, video data of each trial were collected using a digital video camera (JVC-GRDVL9800E; Wayne, NJ, USA) at 60 frames s⁻¹. Video data were used to determine touchdown and toe-off events.

The total positive work that must be supplied by muscles and tendons during locomotion (*W_{tot}*) can be divided into two parts (Fenn, 1930). The first part is the mechanical work required to move body segments relative to the whole-body center of mass (internal work; *W_{int}*). *W_{int}* is calculated from changes in each segment's energy over an entire stride (after Fedak et al., 1982; Willems et al., 1995). The second part of *W_{tot}* is external work (*W_{ext}*); the work that must be supplied to lift and accelerate the whole body center of mass (Cavagna et al., 1977). Power (*W_{int}* and *W_{ext}*) is simply the rate at which internal or external work is done. Alternative approaches to calculating *W_{ext}* will be discussed in a later section.

The kinetic energy of each body segment relative to the body center of mass was calculated from the 3-D marker positions captured by the Vicon motion analysis system. For each stride, one side of the body (side facing cameras or ipsilateral side) was divided into five segments (trunk, arm, forearm, thigh, leg) that were defined by passive reflective markers at each of the major joints. Affixing markers to define the hand and foot segments was problematic both because of the small size of the individuals' hands and feet and because the infant baboons were more likely to remove those markers. For this analysis, the hands and feet were considered point masses at the distal ends of the forearms and lower legs, respectively, and the head was considered a point mass at the cranial end of the trunk. The positions and velocities for segments on the contralateral side of the body were estimated assuming the movements of the contralateral side segments during half a stride were the same as the movements of the ipsilateral segments during the other half of the stride (see Fedak et al., 1982; Willems et al., 1995).

Mass-specific *W_{int}* was calculated as the sum of the positive changes in each limb's kinetic energy per stride divided by body mass (after Willems et al., 1995). Dividing mass-specific *W_{int}* by stride duration gives *W_{int}*. This method of calculating internal work allows for transfers of energy between segments of a single limb but not between limbs. To calculate *W_{ext}*, potential and kinetic energies (both horizontal and vertical) of the body center of mass were summed at each instant in time to obtain the total energy of the center of mass (*E_{cm}*). Center of mass position and velocity were reconstructed based on the positions of limb segment centers of mass (after Minetti et al., 1999). Mass-specific external mechanical work (*W_{ext}*) was calculated as the sum of the positive increments in the *E_{cm}* curve over an entire stride divided by body mass. Mass-specific external power (*W_{ext}*) was calculated as (*W_{ext}*/stride duration).

Manipulation of internal power calculations

A manipulation of inertial properties was performed to examine the sensitivity of *W_{int}* to an individual's limb mass distribution. This manipulation consisted of scaling the segment inertial properties of all subjects with distally light limbs to the inertial properties of the individual with the heaviest distal limb elements. *W_{int}* was recalculated using these scaled values for limb segment inertial properties. The following equations were used to scale segment inertial

properties of older individuals (individual 2) to those of the subject with the heaviest distal limb elements (individual 1):

$$B_{\text{scaled}} = B_2 (M_1/B_1), \quad (3)$$

$$D_{\text{scaled}} = h_2 (D_1/h_1), \quad (4)$$

$$I_{\text{scaled}} = M_2 h_2 (I_1/M_1 h_1^2), \quad (5)$$

where B_1 and B_2 are the body masses of individuals 1 and 2, respectively, M_1 and M_2 are the segment masses of individuals 1 and 2, respectively, h_1 and h_2 are the segment lengths of individuals 1 and 2, D_1 is the segment center of mass position from the proximal end of the segment for individual 1, and I_1 is the segment mass moment of inertia about its center of mass for individual 1.

Data analysis

Comparisons in power outputs between Group 1 and Group 2 infant baboons were performed in two ways. First, analyses of covariance (ANCOVAs) were used to compare variables between groups, with velocity as the covariate since power outputs are correlated with velocity in infant baboons. Since Group 1 and Group 2 individuals differ in size, ANCOVAs were also performed with dimensionless velocity [velocity/(gh)^{0.5}] as the covariate. Significant differences were determined using Tukey–Kramer *post-hoc* tests to account for multiple comparisons. In addition to ANCOVAs, a residuals analysis was performed. Specifically, residuals were calculated from the least-squares regression line relating dimensionless stride frequency [stride frequency/(g/h)^{0.5}] and dimensionless velocity as well as mass-specific internal power and dimensionless velocity. Residual internal power outputs were then regressed on residual stride frequencies. These residuals were calculated from the entire sample (Group 1 and Group 2 combined). A significant positive correlation indicates that those individuals who use high stride frequencies relative to velocity also have high internal power outputs. A similar analysis was performed for external power. Residuals of external power and dimensionless velocity were regressed on residuals of dimensionless stride length (stride length/ h) and dimensionless velocity. A significant positive correlation indicates that those individuals using relatively long strides would also have relatively high external power outputs. All analyses were performed on log-transformed data since the relationship between power outputs and velocity is not linear.

Results

Recently, Raichlen has shown that this sample of infant baboons follows the predicted relationships between limb mass distribution and kinematics (Raichlen, 2005a). The infant baboons show a gradual shift from more distal to more proximal limb mass distribution patterns (Raichlen, 2005b) but, because of limb flexion during swing phase, the infants fall into two main groups, within which $dNPP_{\text{minS}}$ calculated during swing phase do not differ significantly. Group 1

Table 2. Between-group comparisons of kinematics and power outputs in the combined sample

| Variable | LSM1 (95% C.I.) | LSM2 (95% C.I.) | H ₀ |
|-------------------------------|--------------------|--------------------|----------------|
| Stride frequency ¹ | −0.632 (0.008) | −0.580 (0.004) | <0.0001 |
| Stride length ¹ | 0.277 (0.008) | 0.223 (0.004) | <0.0001 |
| Internal power ² | −0.854 (0.098) | −0.795 (0.042) | 0.711 |
| External power ² | −0.142 (0.090) | −0.190 (0.040) | 0.022 |
| Total power ² | −0.060 (0.091) | −0.090 (0.040) | 0.014 |
| Internal power ³ | −0.923 (0.022) | −0.811 (0.011) | <0.0001 |
| External power ³ | −0.203 (0.028) | −0.194 (0.015) | 0.594 |
| Total power ³ | −0.151 (0.031) | −0.145 (0.016) | 0.741 |

LSM1 is the least-squares mean for Group 1 for each variable after dimensionless velocity has been taken into account. LSM2 is the least-squares mean for Group 2 for each variable after dimensionless velocity has been taken into account. 95% confidence intervals are given in parentheses. H₀ is the probability that LSM1 is equal to LSM2.

¹Stride frequencies and stride lengths were made dimensionless, and dimensionless velocity was the covariate.

²Velocity was used as the covariate.

³Dimensionless velocity was used as the covariate.

includes the youngest ages of infant baboons and has significantly more distal limb mass than Group 2, which includes the older ages. Group 1 infants use significantly lower stride frequencies and significantly longer strides than Group 2 individuals (Table 2). Based on these results, a trade-off between internal and external power is possible.

Hypothesis 1: ontogenetic analysis

\dot{W}_{int} does not show significant between-group differences when analyzed using velocity as the covariate but is significantly lower in Group 1 individuals compared with Group 2 over the dimensionless velocity range (Fig. 1A,B; Table 2). \dot{W}_{int} was recalculated for each stride of all Group 2 individuals using scaled segment inertial properties (see Materials and methods). If older individuals had the limb mass distributions of younger individuals, but did not reduce their stride frequencies, they would have had approximately 20% higher \dot{W}_{int} values at a given velocity (Fig. 1C). So, by using low stride frequencies when their mass is most distal, the infant baboons save approximately 20% of the mechanical power they would otherwise have had to output to move their limbs relative to their body.

Group 1 individuals have significantly higher \dot{W}_{ext} over the velocity range, but do not show significant between group differences in \dot{W}_{ext} at a given dimensionless velocity (Fig. 1D,E; Table 2). Finally, \dot{W}_{tot} is larger in Group 2 individuals at a given velocity but does not show significant between-group differences in the combined sample of infant baboons over the dimensionless velocity range (Fig. 1F,G; Table 2). Between-group differences in body size must be taken into account because the same velocity has different impacts on individuals with different limb lengths (Alexander

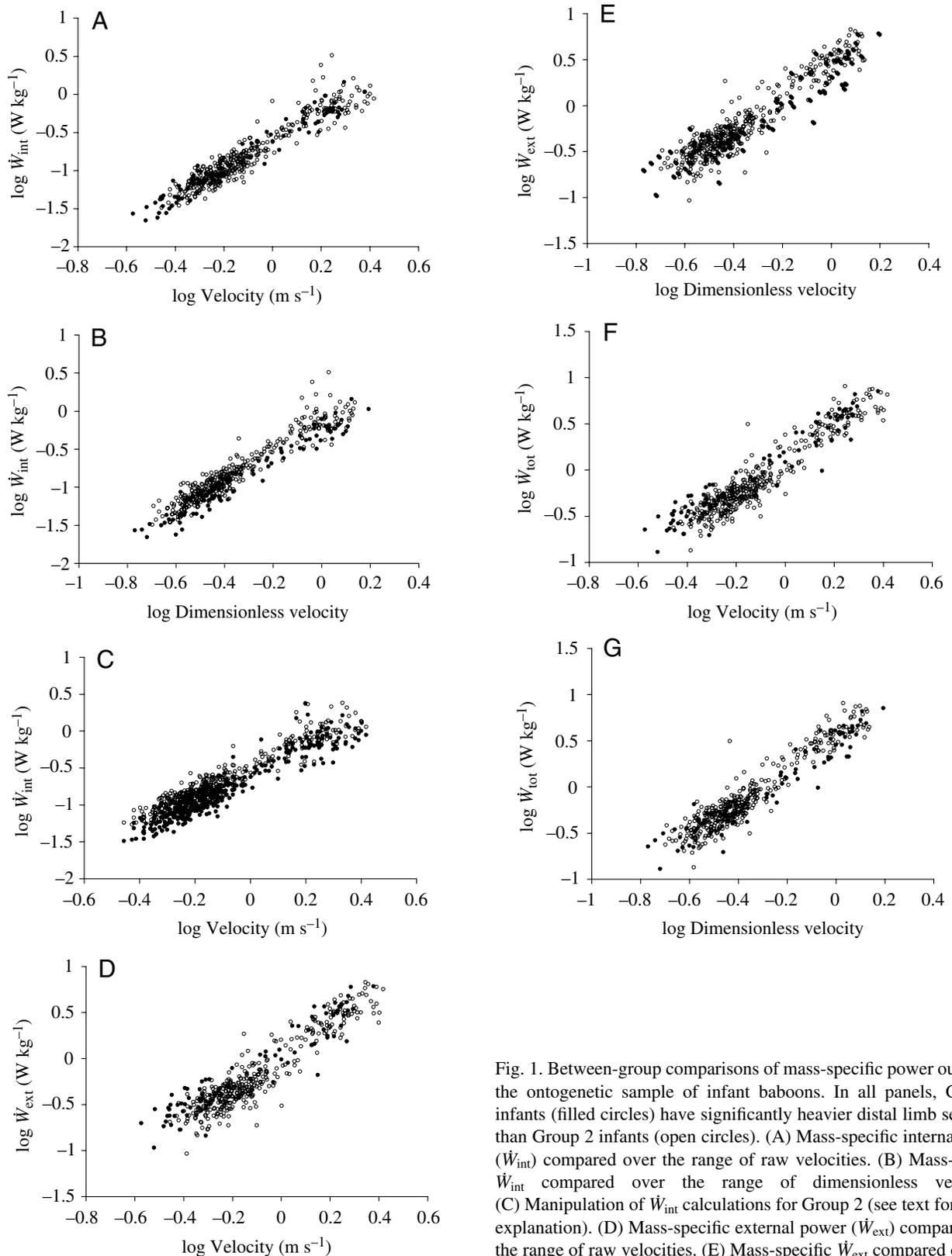


Fig. 1. Between-group comparisons of mass-specific power outputs in the ontogenetic sample of infant baboons. In all panels, Group 1 infants (filled circles) have significantly heavier distal limb segments than Group 2 infants (open circles). (A) Mass-specific internal power (\dot{W}_{int}) compared over the range of raw velocities. (B) Mass-specific \dot{W}_{int} compared over the range of dimensionless velocities. (C) Manipulation of \dot{W}_{int} calculations for Group 2 (see text for further explanation). (D) Mass-specific external power (\dot{W}_{ext}) compared over the range of raw velocities. (E) Mass-specific \dot{W}_{ext} compared over the range of dimensionless velocities. (F) Mass-specific total power (\dot{W}_{tot}) compared over the range of raw velocities. (G) Mass-specific \dot{W}_{tot} compared over the range of dimensionless velocities. Statistical between-group differences using ANCOVAs were found for B, D and F. These results can be found in Table 2.

and Jayes, 1983), so the results of the dimensionless velocity comparisons hold greater significance in this study. Although the between-group comparisons of \dot{W}_{int} , \dot{W}_{ext} and \dot{W}_{tot} do not support a trade-off mechanism when examined over the range of dimensionless velocities because \dot{W}_{ext} did not differ between groups, they do support the hypothesis that differences in kinematics between individuals who differ in limb mass distributions will be associated with similar total power outputs.

Individual baboon between-group comparisons generally follow the trends of the combined sample analysis, although the differences are not always significant (Table 3). Only Infant 1 shows significantly lower Group 1 values of \dot{W}_{int} . Although least-squares mean \dot{W}_{int} is lower in Group 1 for the other two individuals, these differences were not significant. For all other variables, the individuals follow the combined-sample results.

Because ANCOVA results may have been compromised by only slight differences in kinematics and power outputs, a residuals analysis was performed. Residuals of dimensionless stride frequency and dimensionless velocity were regressed against residuals of \dot{W}_{int} and dimensionless velocity (Fig. 2A). A significant positive correlation ($r=0.48$; $P<0.001$) indicates that those individuals who have relatively low dimensionless stride frequencies at a given dimensionless velocity have relatively low \dot{W}_{int} at a given dimensionless velocity. Note also that groups cluster together, with Group 1 clustering in

Table 3. Between-group comparisons of power outputs in infants 1–3

| Variable | Group | LSM (95% C.I.) | H_0 |
|------------------------|------------------|-------------------|---------|
| \dot{W}_{int} | Infant 1 Group 1 | -1.195 (0.114) | <0.0001 |
| | Infant 1 Group 2 | -0.873 (0.071) | |
| | Infant 2 Group 1 | -0.735 (0.047) | 0.234 |
| | Infant 2 Group 2 | -0.703 (0.024) | |
| | Infant 3 Group 1 | -0.822 (0.037) | 0.076 |
| | Infant 3 Group 2 | -0.864 (0.014) | |
| \dot{W}_{ext} | Infant 1 Group 1 | -0.304 (0.105) | 0.269 |
| | Infant 1 Group 2 | -0.235 (0.065) | |
| | Infant 2 Group 1 | -0.098 (0.039) | 0.531 |
| | Infant 2 Group 2 | -0.084 (0.020) | |
| | Infant 3 Group 1 | -0.259 (0.051) | 0.745 |
| | Infant 3 Group 2 | -0.250 (0.018) | |
| \dot{W}_{tot} | Infant 1 Group 1 | -0.307 (0.109) | 0.094 |
| | Infant 1 Group 2 | -0.197 (0.068) | |
| | Infant 2 Group 1 | -0.002 (0.036) | 0.444 |
| | Infant 2 Group 2 | 0.014 (0.018) | |
| | Infant 3 Group 1 | -0.261 (0.051) | 0.947 |
| | Infant 3 Group 2 | -0.262 (0.018) | |

All ANCOVAs were performed with dimensionless velocity as the covariate.

LSM, least-squares mean; \dot{W}_{int} , internal power; \dot{W}_{ext} , external power; \dot{W}_{tot} , total power.

H_0 is the probability that the LSM for Group 1 is equal to the LSM for Group 2.

negative residual space (both negative dimensionless stride frequency residuals and negative \dot{W}_{int} residuals). The same analysis of residual stride lengths and \dot{W}_{ext} also shows a slight, but significant, positive correlation between regressed residuals (Fig. 2B; $r=0.21$; $P<0.001$). This relationship is, however, quite weak, suggesting that \dot{W}_{ext} may not be sensitive to slight differences in stride length. Infant baboons show the same patterns when examined individually (Table 4). The residuals for \dot{W}_{int} and stride frequency are more highly correlated than those of \dot{W}_{ext} and stride length, although all correlations are significant.

Hypothesis 2: comparisons with other quadrupeds

To assess the likelihood that larger differences in inertial properties and kinematics lead to power output trade-offs, the

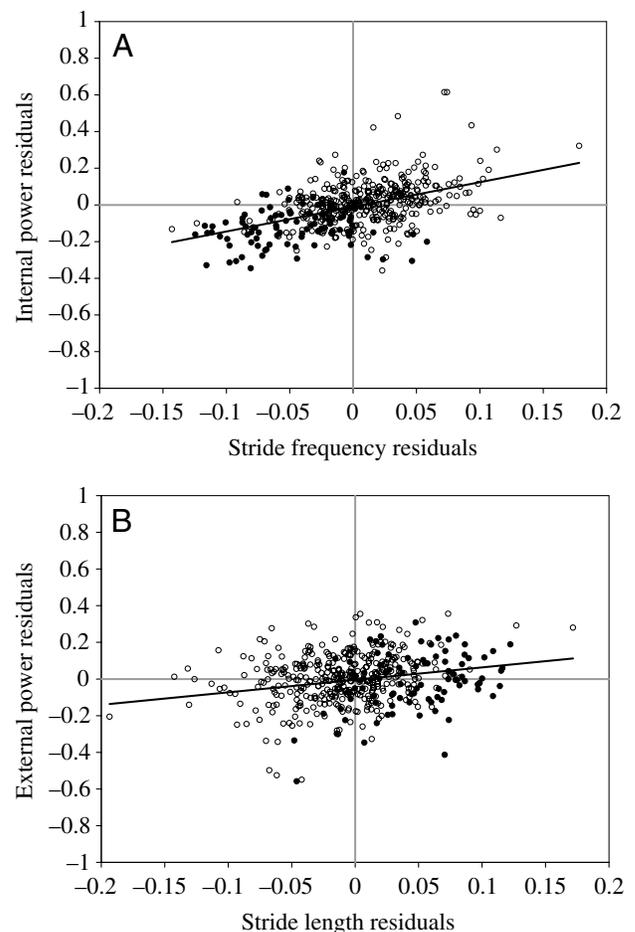


Fig. 2. Residuals analysis of kinematics and mechanical power. (A) Residuals of internal power vs dimensionless velocity regressed on residuals of dimensionless stride frequency vs dimensionless velocity ($r=0.48$; $P<0.001$). Group 1 is represented by filled circles and Group 2 is represented by open circles. Note that Group 1 clusters together in the negative residuals quadrant. (B) Residuals of external power vs dimensionless velocity regressed on residuals of dimensionless stride length vs dimensionless velocity ($r=0.21$; $P<0.001$). Group 1 is represented by filled circles and Group 2 is represented by open circles. Note that Group 1 clusters in the positive residuals quadrant.

Table 4. Residuals analysis of kinematics and power outputs in the individual infant baboons

| Infant | Residual regression | <i>r</i> | <i>P</i> |
|--------|------------------------------|----------|----------|
| 1 | \dot{W}_{int} vs SF | 0.37 | <0.0001 |
| 2 | \dot{W}_{int} vs SF | 0.59 | <0.0001 |
| 3 | \dot{W}_{int} vs SF | 0.29 | <0.0001 |
| 1 | \dot{W}_{ext} vs SL | 0.36 | <0.0001 |
| 2 | \dot{W}_{ext} vs SL | 0.23 | 0.003 |
| 3 | \dot{W}_{ext} vs SL | 0.19 | 0.009 |

Residuals were calculated from least-squares regression lines relating each variable with dimensionless velocity.

SF, stride frequency; SL, stride length; \dot{W}_{int} , internal power; \dot{W}_{ext} , external power.

infant baboons (combined Group 1 and Group 2) were compared with more cursorial non-primate quadrupeds. In the following comparative analyses, dogs and horses are used because data for inertial properties, kinematics and power outputs in these species are readily available in the literature.

Inertial properties for dogs were taken from Myers and Steudel (1997) and for horses from Buchner et al. (1997). Stride frequencies and stride lengths were calculated from equations in Minetti et al. (1999) for horses and from Williams et al. (2002) for dogs. Power outputs for dogs were taken from Heglund et al. (1982b) and Fedak et al. 1982), and power for horses was taken from Minetti et al. (1999). ANCOVAs cannot be used to compare non-primate kinematics and power outputs with those of the infant baboons because only least-squares regression equations relating kinematics and power to velocity in dogs and horses have been reported. Therefore, the 95% confidence intervals of the regression lines for the infant baboon sample were calculated and differences are suggested when the regression line for the non-primate data set fell outside of this interval. The limb length used to calculate dimensionless velocity for dogs was given in Williams et al. (2002) for kinematics and Fedak et al. (1982) for power. For the horse data set, limb length was estimated from allometric equations in Alexander et al. (1979) for mean horse body mass in Minetti et al. (1999) (limb length = 1.26 m).

Infant baboons have more distal forelimb and hindlimb centers of mass compared with dogs and horses (Table 5). Following the predicted relationships between inertial properties and kinematics, infant baboons use lower stride frequencies and longer strides at a given dimensionless velocity than either dogs or horses (Fig. 3A,B). The infant baboon sample has lower \dot{W}_{int} (Fig. 3C) and higher \dot{W}_{ext} compared with the non-primates (Fig. 3D). The lower \dot{W}_{int} and higher \dot{W}_{ext} in the infant baboons lead to similar \dot{W}_{tot} in the infant baboon sample compared with the non-primate sample (Fig. 3E). These data are consistent with the presence of a trade-off mechanism where low stride frequencies are associated with relatively low internal power, long strides are

Table 5. Center of mass positions as a fraction of limb length (95% C.I.) in the infant baboons, dogs and horses

| Variable | <i>Papio</i> (<i>N</i> =3) | <i>Canis</i> (<i>N</i> =10) | <i>Equus</i> (<i>N</i> =6) |
|-------------------|--------------------------------|---------------------------------|--------------------------------|
| Hindlimb <i>D</i> | 0.410 (0.007) | 0.304 (0.023) | 0.327 |
| Forelimb <i>D</i> | 0.467 (0.005) | 0.342 (0.068) | 0.343 |

Data for *Canis* (Myers and Steudel, 1997); data for *Equus* (Buchner et al., 1997).
N, number of animals; *D*, distance of the center of mass from the proximal joint.

associated with high external power, and total power does not differ significantly among the sampled taxa.

Discussion

Superficially, the results from the ontogenetic sample do not support the idea that differences in stride frequency and stride length among animals with different limb mass distributions will have opposite effects on \dot{W}_{int} and \dot{W}_{ext} . Although relatively low stride frequencies are associated with low \dot{W}_{int} , the relationship between stride length and \dot{W}_{ext} appears to be less clear.

The comparison of mechanical power in infant baboons with dogs and horses is, however, consistent with the presence of a mechanical power trade-off mechanism. The infant baboons have more distally heavy limbs and use longer strides and lower stride frequencies compared with dogs and horses. The infant baboons do less \dot{W}_{int} and more \dot{W}_{ext} compared with the dog and horse samples, and their values of \dot{W}_{tot} do not differ significantly from those of the non-primate sample. It is possible that the trade-off mechanism is only apparent when stride frequencies and stride lengths differ greatly between taxa.

There are several possible reasons for the absence of trade-offs in the ontogenetic sample despite the presence of a trade-off mechanism in the inter-specific sample. First, the differences in inertial properties between infant groups were smaller than inter-specific differences. Perhaps slight differences in spatio-temporal kinematics simply equalize energy outputs, rather than having the trade-off effects. This possibility seems likely given the results of the manipulation of internal power calculations (see Fig. 1C). If young infants, with their relatively distally heavy limbs, used the kinematics of older aged infants, \dot{W}_{int} would be approximately 20% higher.

Second, it is possible that the kinematic method of calculating center of mass displacement is not sensitive enough to make comparisons within small differences in stride length. Future examinations of the trade-off mechanism could use force-plate data to calculate center of mass displacements, although Gard et al. (2004) suggest that differences between the two techniques are minimal.

Finally, it is possible that \dot{W}_{ext} , as calculated here, does not fully account for the power output to produce center of mass

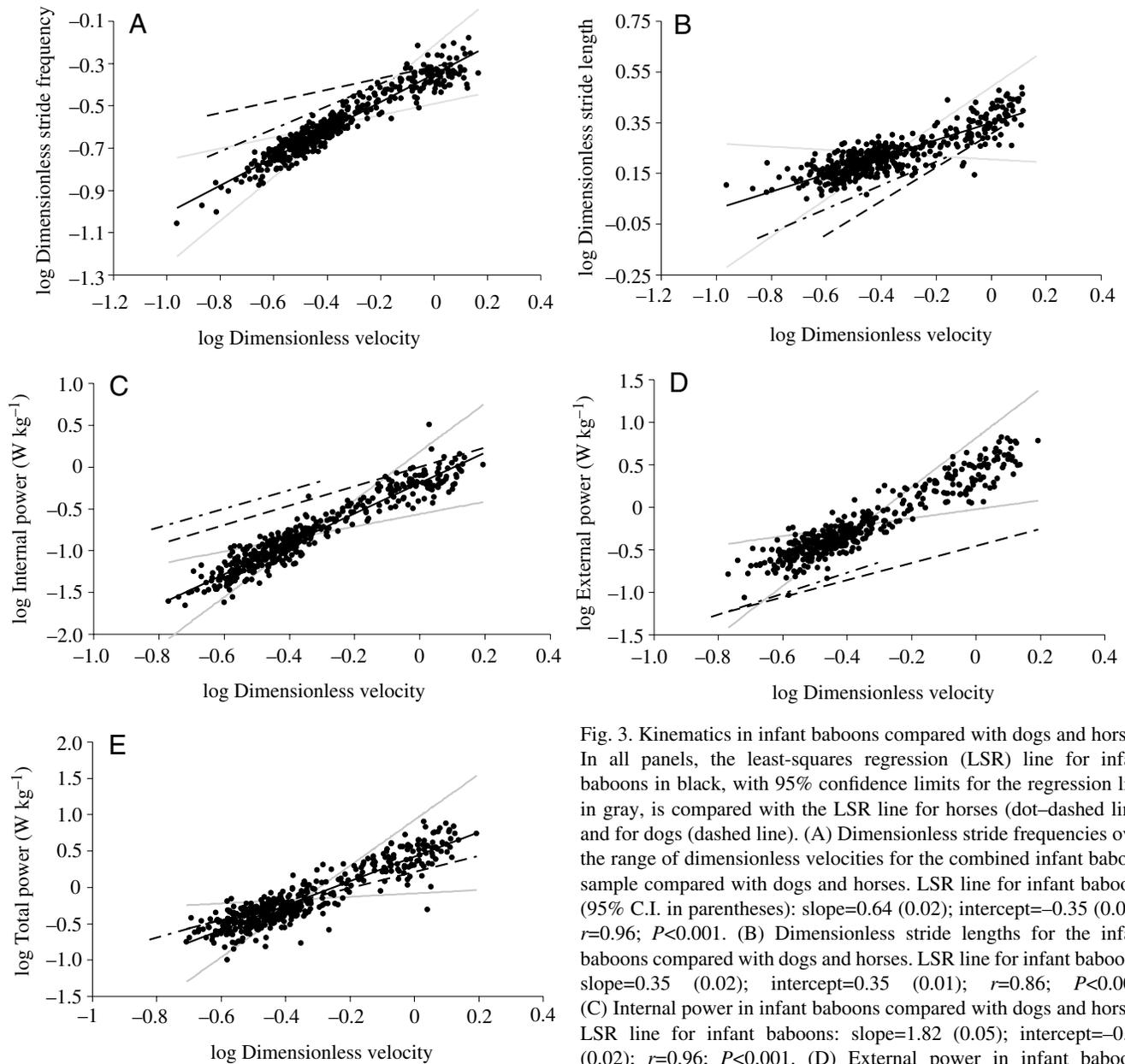


Fig. 3. Kinematics in infant baboons compared with dogs and horses. In all panels, the least-squares regression (LSR) line for infant baboons in black, with 95% confidence limits for the regression line in gray, is compared with the LSR line for horses (dot-dashed line) and for dogs (dashed line). (A) Dimensionless stride frequencies over the range of dimensionless velocities for the combined infant baboon sample compared with dogs and horses. LSR line for infant baboons (95% C.I. in parentheses): slope=0.64 (0.02); intercept=-0.35 (0.01); $r=0.96$; $P<0.001$. (B) Dimensionless stride lengths for the infant baboons compared with dogs and horses. LSR line for infant baboons: slope=0.35 (0.02); intercept=0.35 (0.01); $r=0.86$; $P<0.001$. (C) Internal power in infant baboons compared with dogs and horses. LSR line for infant baboons: slope=1.82 (0.05); intercept=-0.19 (0.02); $r=0.96$; $P<0.001$. (D) External power in infant baboons compared with dogs and horses. LSR line for infant baboons: slope=1.68 (0.06); intercept=0.37 (0.03); $r=0.92$; $P<0.001$. (E) Total power in infant baboons compared with dogs and horses. LSR line for infant baboons: slope=1.68 (0.07); intercept=0.42 (0.03); $r=0.92$; $P<0.001$.

motion. Recently, Donelan et al. (2002) suggested that much of the work required to produce center of mass motion actually occurs as the center of mass is redirected at the end of the stance phase during walking (e.g. collisional costs; see also Bastien et al., 2003 for alternative method of calculating this cost). This work done during the double-contact phase of walking may represent a substantial portion of \dot{W}_{ext} and should scale with step length⁴ (Donelan et al., 2002). If true, then \dot{W}_{ext} as measured here does not fully account for the effects of longer strides on the power required to lift and accelerate the center of mass.

Infant baboons do show between-group differences in dimensionless step length (ANOVA results: Group 1 mean=0.94, Group 2 mean=0.88, $P<0.001$, $F=3.86$), which should lead to higher step-to-step costs in Group 1 infants. In fact, Group 1 step lengths raised to the fourth power (mean=0.78) are 23% higher than those of Group 2 (mean=0.59). This value is quite similar to the between-group difference in least-squares means for \dot{W}_{int} (22%; see Table 2). Although differences in center of mass height changes associated with longer strides may not be large enough to impact ontogenetic changes in \dot{W}_{ext} as calculated in this study,

ontogenetic differences in step-to-step costs may in fact provide the trade-off.

Although the results presented above suggest a trade-off in mechanical costs, the relationship between mechanical and metabolic costs remains unclear. In a classic paper, Heglund et al. showed a disconnection between mechanical power and metabolic costs of locomotion in a wide range of taxa (Heglund et al., 1982a). This disconnection is due to the fact that muscles consume energy not only when they do work but also when they produce force isometrically (Kram and Taylor, 1990). Despite the large impact of isometric force production on metabolic costs of locomotion, increases in mechanical power at a given speed (driven by changes in stride frequency/length at a given speed) cause an increase in metabolic cost (Minetti et al., 1995). Thus, minimizing total power should reduce the metabolic costs of locomotion at a given speed. Minetti et al. (1999) suggest that a complete description of metabolic costs should therefore include a combination of mechanical work and power plus the costs associated with isometric muscle force production.

Implications for mammalian limb design

These results may explain why mammals in general do not differ greatly in energy costs despite differences in limb mass distributions. Taylor et al. (1974) showed that the cheetah, the gazelle and the goat do not differ in their energetic costs despite having different limb mass distributions. Domestic cats use relatively longer strides than other mammalian cursors (see fig. 3 in Alexander and Jayes, 1983), and these long strides may be linked to their distally heavy limbs. If cheetahs use similar kinematics, then low stride frequencies and long strides may explain their similar energetic costs compared with the goat and gazelle. Cheetahs' low stride frequencies and long strides would reduce their internal power outputs while increasing their external power outputs, allowing them to maintain similar total power outputs compared with other mammals.

It is possible that all mammals follow a similar trade-off pattern that is dependent on their limb mass distributions. Alexander and Jayes (1983) showed that non-cursorial mammals use longer strides at a given dimensionless velocity compared with more cursorial mammals. Since non-cursors also have more distal limb mass concentrations than cursors (Grand, 1977; Myers and Steudel, 1997; Raichlen, 2004), non-cursors may be taking advantage of the trade-off mechanism to reduce total mechanical power.

The trade-off mechanism may have played an important role in allowing mammalian quadrupeds to evolve non-locomotor functions in their distal limb elements that would increase distal mass, without having a negative impact on their energy costs of locomotion. This type of mechanism would have been especially important for animals such as primates, who rely on their distally heavy limb muscles to control their grasping hands and feet. Grasping hands and feet are a hallmark of the primate order and were an essential element of the success of early primates (Cartmill, 1972). The use of the trade-off

mechanism would have allowed early primates to evolve grasping hands and feet without exacting an energetic price.

Why concentrate limb mass proximally?

Although the results from this study suggest that mechanisms exist that reduce the impact of limb mass distributions on mechanical power outputs, the question of why cursorial mammals concentrate limb mass proximally remains unanswered. Based on the available evidence from studies of energy costs of transport in mammals, proximally concentrated limb mass does not lead to greatly reduced energy expenditures (Taylor et al., 1974; Taylor et al., 1982; Heglund, 1985). Other adaptive scenarios must therefore be examined.

Reducing distal limb mass leads to a reduction in the limb's mass moment of inertia (e.g. the limb's resistance to rotational acceleration). Limb mass moments of inertia affect limb acceleration relative to the body and therefore affect whole-body accelerations (Ropret et al., 1998; Pasi and Carrier, 2003; Rahmani et al., 2003). Although it seems clear that the ability to sprint at high speeds is determined mainly by the ability to produce greater ground reaction forces (Weyand et al., 2000), studies of lower limb loading show significant reductions in limb velocity and consequently reductions in maximum sprint velocity with added distal loads (Ropret et al., 1998).

Accelerations are necessary to either catch prey or evade predators (Elliott et al., 1977), and thus structures that enhance an individual's ability to accelerate should be subjected to large selection pressures. Since the ability to rapidly accelerate is a strong predictor of successful predator evasion in many taxa (Elliott et al., 1977), the evolution of proximal limb mass may be the result of selection for acceleration capabilities. Although the results from the present study certainly cannot address why cursorial quadrupeds concentrate limb mass proximally, the context of predator-prey interactions may provide selection pressures for the evolution of proximally concentrated limb mass.

Summary

Infant baboons show some ontogenetic evidence of a trade-off mechanism, although the relationship between external power and stride length appears to be weak. Compared with dogs and horses, the infant baboon sample has lower internal power outputs, higher external power outputs and more similar total power outputs. These results suggest that, on a broad scale, individuals may use a combination of stride frequency and stride length that is determined by their limb mass distributions and that minimizes total mechanical power outputs. These findings suggest that selection pressures for non-cursorial activities acting on the distal limb elements of primates, and perhaps other mammals in general, do not have to exact an energetic price. Quadrupeds may adjust their kinematics to accommodate limb mass distribution patterns that, superficially, seem detrimental to quadrupedal energetics. Additionally, the results from this study suggest that researchers should explore new explanations for the evolution of proximally concentrated limb mass in cursorial quadrupeds.

List of symbols

| | |
|------------------------|---|
| D | distance of limb center of mass from the proximal end |
| $dNPP$ | dimensionless natural pendular period |
| $dNPP_{\min}$ | minimum $dNPP$ during swing phase for a given stride |
| E_{cm} | total energy of the body center of mass |
| h | limb length |
| I | mass moment of inertia of the limb about a transverse axis through its proximal joint |
| B | body mass |
| M | segment mass |
| NPP | limb natural pendular period |
| W_{int} | internal work |
| \dot{W}_{int} | internal power |
| W_{ext} | external work |
| \dot{W}_{ext} | external power |
| W_{tot} | total work |
| \dot{W}_{tot} | total power |

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