

Morphological Conservation of Limb Natural Pendular Period in the Domestic Dog (*Canis familiaris*): Implications for Locomotor Energetics

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ABSTRACT For better understanding of the links between limb morphology and the metabolic cost of locomotion, we have characterized the relationships between limb length and shape and other functionally important variables in the straightened forelimbs and hindlimbs of a sample of 12 domestic dogs (*Canis familiaris*). Intra-animal comparisons show that forelimbs and hindlimbs are very similar (not significantly different) in natural pendular period (NPP), center-of-mass, and radius of gyration, even though they differ distinctly in mass, length, moment-of-inertia, and other limb proportions. The conservation of limb NPP, despite pronounced dissimilarity in other limb characteristics, appears to be the result of systematic differences in shape, forelimbs tending to be cylindrical and hindlimbs conical. Estimating limb NPP for other species from data in the literature on segment inertia and total limb length, we present evidence that the similarity between forelimbs and hindlimbs in NPP is generally true for mammals across a large size range. Limbs swinging with or near their natural pendular periods will maximize within-limb pendular exchange of potential and kinetic energy. As all four limbs of moderate- and large-size animals swing with the same period during walking, maximal advantage can be derived from the pendular exchange of energy only if forelimbs and hindlimbs are very similar in NPP. We hypothesize that an important constraint in the evolution of limb length and shape is the locomotor economy derived from forelimbs and hindlimbs of similar natural pendular period. *J. Morphol.* 234:183–196, 1997. © 1997 Wiley-Liss, Inc.

Limbs and their movements are central elements of terrestrial locomotion in mammals. Aspects of limb morphology that have been studied and discussed include: scaling of limb parameters (e.g., Alexander, '77; Alexander et al., '79; Biewener, '83; Steudel and Beattie, '93), effect of distribution of limb mass on the cost of locomotion (artificial loads: Myers and Steudel, '85; Martin, '85; Steudel, '90a; Myers et al., '93; natural variation in shape: Howell, '44; Taylor et al., '74; Hildebrand and Hurley, '85), limb and limb segment lengths as predictors of maximal running speed (Garland and Janis, '93) or locomotor efficiency (e.g., Klein et al., '87; Kram and Taylor, '90; Janis and Wilhelm, '93; Steudel and Beattie, '95), and limb inertia or length as determinants of stride times or lengths (Alexander and Jayes, '83; Turvey et al., '88; Witte et al., '91).

Notwithstanding this scrutiny, we still do not fully understand the role of limb morphology in determining the cost to an animal during walking or running. Part of the problem with answering this question is that many morphological and kinematic characteristics are highly correlated with one another, making it hard to discriminate between causative and correlative factors (Myers et al., '93; Steudel and Beattie, '95). Is this pervasive co-linearity the result of evolutionary convergence of limb structure and function to produce an optimally tuned system? Are these coupled relationships determined by underlying physical laws? One way of approaching these questions is to

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study the behavior of experimentally altered limb systems (e.g., Martin, '85; Myers and Steudel, '85; Steudel, '90a,b; Myers et al., '93; Webb et al., '94). Another useful strategy is to examine natural variation in limb morphology or function that partially uncouples factors that are normally observed in tight correlation (e.g., Taylor et al., '74; Klein et al., '87).

The present study is an example of the latter method of investigation in that we have looked for evidence of functional similarities despite marked morphological variability within and between members of a single species—the domestic dog (*Canis familiaris*). Because this species has been selectively bred, our sample shows a relatively large range of variation in limb mass, length, and shape. In this context, we have compared characteristics of the straightened forelimbs and hindlimbs of each animal to see if they have converged for the two limb types, as a response to all four limbs having common functional constraints during locomotion.

A functionally significant limb characteristic that we have examined is the natural pendular period (NPP) of the straightened limbs. An important energy-saving mechanism thought to be operating in humans and animals, especially during walking, is the pendular exchange of potential and kinetic energy as the limbs swing back and forth during a stride (Mochon and McMahon, '80; Hildebrand, '85; Pandy and Berme, '88). The NPP of a swinging limb "pendulum" is the period of oscillation at which exchange between potential and kinetic energy is maximal, and the metabolic energy required to maintain swinging is minimal. The energy required to maintain steady-state swinging in a pendular system is proportional to $1 - \{(\text{observed period})^2 / (\text{natural period})^2\}$ (Hildebrand, '85; Swartz, '89). In addition, a limb oscillating at other than its NPP will exhibit increased fluctuations of amplitude and duration from swing to swing (Rosenblum and Turvey, '88). This means an animal's cost of locomotion should increase significantly when the swing period differs, even a small amount, from the NPP of the limb. All four limbs of moderate size (ground squirrel) and larger quadrupeds have been shown to have the same swing period (Arshavskii et al., '65; Alexander and Jayes, '83; Biewener, '83). In order to maximize the pendular exchange of potential and kinetic energy within the ro-

tating limbs, the NPP of all four limbs of quadrupeds also should match closely. Based on empirical determination of the NPP of straightened forelimbs and hindlimbs, we have tested whether this is the case for the dogs in our sample.

To argue that an observed convergence of NPP has evolved as part of a finely tuned system that minimizes the cost of locomotion, we must provide evidence that any similarities in NPP are not merely the result of animals having forelimbs and hindlimbs of more or less the same length. Consequently, we have examined the influence of limb length and shape on NPP and whether NPP is similar between forelimbs and hindlimbs in other species.

Another functional constraint shared by forelimbs and hindlimbs is the need to minimize the muscle forces that must be generated to produce the mechanical work of locomotion. These forces will be reduced by either a decrease in limb mass, or a change in limb shape to a more proximal allocation of limb mass. To see whether forelimbs and hindlimbs show similar adaptations that minimize the mechanical work of locomotion, we have measured the mass, center-of-mass, and moment-of-inertia of the straightened limbs of our study dogs. We have also characterized the relationship between total limb inertia and limb length in both forelimbs and hindlimbs.

MATERIALS AND METHODS

Animals

Body masses and breeds (if known) of the 12 adult domestic dogs (*Canis familiaris*) used in our study are reported in Table 1. All animals were obtained from local veterinarians or the University of Wisconsin Medical School immediately after death. An attempt was made to have a good range of both body mass and limb morphology represented in the sample. The breeds and breed mixtures represented have all been bred for tasks (hunting, retrieving, coaching) in which locomotor endurance is important. Body mass was measured either just before or just after death. None of the animals had experienced any treatment or disease that would alter their limb structure or total body mass.

Dismemberment procedure and limb measurements

The protocols for dismemberment and determination of limb center-of-mass (CM) and

TABLE 1. Body mass, forelimb (FL), and hindlimb (HL) parameters for each dog¹

| Dog no. | Dog type | Body mass (BM) [kg] | Limb mass (LM) [gm] | | Limb inertia (I) [gm-m ²] | | Total limb length (TL) [cm] | | Limb center of mass (CM) [cm] | | Radius of gyration (RG) [cm] | | Natural pendular period (NPP) [s] | |
|---------|-----------|---------------------|---------------------|------|---------------------------------------|-------|-----------------------------|------|-------------------------------|------|------------------------------|------|-----------------------------------|-------|
| | | | FL | HL | FL | HL | FL | HL | FL | HL | FL | HL | FL | HL |
| 1 | Mongrel | 21.3 | 963 | 1657 | 31.50 | 53.80 | 44.7 | 51.7 | 14.0 | 13.9 | 18.1 | 18.0 | 0.970 | 0.970 |
| 2 | Beagle | 11.7 | 388 | 505 | 3.44 | 6.53 | 26.1 | 28.0 | 7.0 | 8.9 | 9.4 | 11.4 | 0.714 | 0.765 |
| 3 | Beagle | 17.0 | 563 | 712 | 8.66 | 12.10 | 28.3 | 32.5 | 9.2 | 10.1 | 12.4 | 13.0 | 0.821 | 0.823 |
| 4 | Mongrel | 11.5 | 466 | 792 | 13.80 | 21.90 | 37.4 | 43.1 | 13.4 | 12.7 | 17.2 | 16.6 | 0.944 | 0.937 |
| 5 | Mongrel | 18.4 | 959 | 1416 | 46.70 | 73.90 | 47.5 | 55.1 | 17.4 | 18.1 | 22.1 | 22.8 | 1.062 | 1.078 |
| 6 | Mongrel | 12.4 | 516 | 774 | 11.70 | 20.80 | 35.8 | 41.6 | 11.5 | 12.8 | 15.1 | 16.4 | 0.891 | 0.920 |
| 7 | Mongrel | 13.1 | 527 | 870 | 15.70 | 25.30 | 38.0 | 42.3 | 13.6 | 13.3 | 17.3 | 17.1 | 0.939 | 0.939 |
| 8 | Mongrel | 23.8 | 852 | 1660 | 35.90 | 61.40 | 45.8 | 51.8 | 16.8 | 14.6 | 20.5 | 19.2 | 1.005 | 1.010 |
| 9 | Beagle | 10.7 | 412 | 690 | 10.70 | 17.20 | 36.0 | 39.3 | 12.6 | 12.6 | 16.1 | 15.8 | 0.911 | 0.893 |
| 10 | Mongrel | 13.9 | 583 | 840 | 19.50 | 23.60 | 38.2 | 42.7 | 14.2 | 13.2 | 18.3 | 16.8 | 0.974 | 0.926 |
| 11 | Mongrel | 23.6 | 914 | 1375 | 37.10 | 54.70 | 45.5 | 53.6 | 16.1 | 16.0 | 20.1 | 19.9 | 1.008 | 1.001 |
| 12 | Dalmatian | 19.0 | 725 | 1104 | 24.90 | 35.40 | 42.7 | 47.5 | 14.8 | 14.1 | 18.5 | 17.9 | 0.967 | 0.957 |

¹All limb data were taken on straightened limbs from the right side.

limb moment-of-inertia (I) were generally patterned after those used by Vilenky ('79) for whole limbs. We measured all limb variables on straightened limbs (joints extended). This configuration was easy to replicate from limb to limb and represented the largest value possible for length-related variables. This limb position closely approximates the orientation of the limb throughout a significant fraction of the stride during walking (Goslow et al., '81; Hildebrand, '85). However, dogs do flex their limbs to some extent during a stride, even when walking. To determine whether the NPP of flexed forelimbs and hindlimbs of locomoting dogs should be as similar as that of straightened limbs, we examined: (1) how much limb NPP differs between the straightened and fully flexed orientation, and (2) how similar the degree of flexion is in the forelimb and hindlimb during the swing phase. This analysis showed that limb NPP was reduced only a small amount by the most extreme flexion observed during walking and that both the amount and duration of forelimb and hindlimb flexion during the swing phase of walking is quite similar (see Discussion for details). All limb variables were measured on forelimbs and hindlimbs from the right side of each dog, as we assumed differences between the left and right limbs of an animal were slight.

Soon after obtaining the cadaver, we measured total limb length (TL) while holding the limbs in the straightened position. Forelimb TL was measured from the spot between the acromion process of the scapula and the greater tubercle of the humerus to the tip of the fore paw. Hindlimb TL was

measured from the position between the ischial tuberosity and the greater trochanter of the femur to the tip of the hind paw.

We did not include the scapula as part of the forelimb. Because dogs have only rudimentary clavicles, the scapulae have no joint connections with the upper thorax and are instead attached to the axial skeleton and held in place by four large flat muscles (Adams, '86). This arrangement allows the lower edge of the scapula to be pulled forward slightly by muscles during the swing period. However, the forelimb is only able to swing freely (as is necessary for effective pendular motion) from the diarthrotic, ball-and-socket joint between the humerus and the scapula—where the geometry of the joint and the synovial fluid reduce the damping frictional forces.

To determine the correct place to cut the limbs from the trunk, the gleno-humeral and hip joints were located by palpation. From these points, a line marking the location of cuts was drawn around the limb, staying as close as possible to the body wall. Next, a scalpel was used to cut through the soft tissue along this line, separating limb tissue from that of the trunk. The limbs were separated from the body by cutting through the ligaments supporting the proximal joint. We did not cut through the head of the femur or humerus as was done by Vilenky ('79). The disarticulated limbs were then weighed and the masses recorded.

After weighing, the limb was tied in the straightened position to a board. The board-limb combination was then placed in a freezer until the limb was frozen into a single rigid body. Freezing was necessary so that

the limb would swing as a single rigid physical pendulum when we empirically determined its swing period. Once frozen, the limb was removed from the board and weighed again. Limb mass loss due to freezing was negligible (1.3% loss in the forelimbs, 1.0% loss in the hindlimbs). The post-freezing limb mass (LM) was the value used in all calculations and analyses.

After the second weighing, the following length and circumference measurements were taken on each forelimb (FL) and hindlimb (HL): *distal segment length (DL)* FL—distance from the pisiform to the tip of the paw, HL—distance from the calcaneum to the tip of the paw; *mid + distal segment length (MDL)* FL—distance from the olecranon process of the ulna to the tip of the paw, HL—distance from the intercondylar tubercle of the tibia to the tip of the paw; *midjoint circumference (MJC)* FL—circumference of the limb just superior to the olecranon process, HL—circumference of the limb measured between the patella and the tuberosity of the tibia; *distal joint circumference (DJC)* FL—circumference of the limb just superior to the styloid processes of the ulna and radius, HL—circumference of the limb just superior to the calcaneum.

After these limb lengths and circumferences were measured, the following lengths were calculated from them: *proximal segment length (PL)* = TL - MDL; *midsegment length (ML)* = MDL - DL; *proximal + mid segment length (PML)* = PL + ML.

Center-of-mass determination

The center-of-mass (CM) of each limb was determined by placing the frozen limb lengthwise on a light-weight metal balancing tray and manipulating the position of the limb until the tray balanced on its fulcrum. A line was then drawn on the segment at the balance point and the distance from the proximal joint to this line (CM) was measured.

Determination of moment-of-inertia, radius of gyration, and natural pendular period

Once LM and CM were measured, the moment-of-inertia about the proximal end (I) was determined for each rigid, straightened limb using a metal pendulum device (Fig. 1). The device was composed of a long thin metal rectangle suspended at one end from a bolt protruding horizontally from a vertically oriented hollow steel column. The

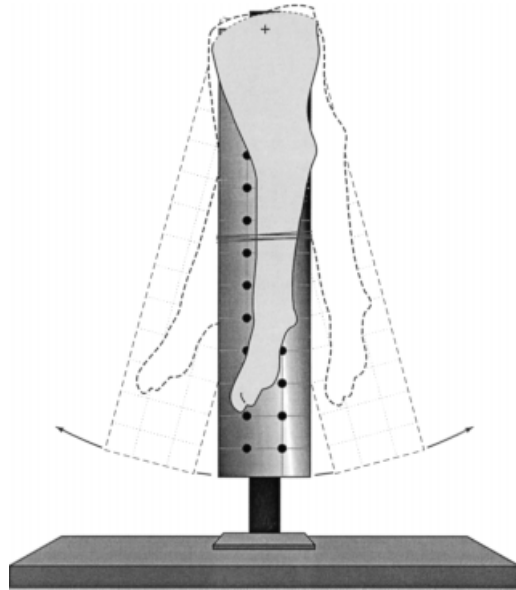


Fig. 1. Drawing of the metal pendulum device used to determine limb natural pendular period. Shown with limb suspended from the bolt which is the center of rotation of the device (denoted with a +).

base of the column was attached to a heavy metal platform for support. This arrangement allowed the metal pendulum to swing freely about the bolt. A small hole was drilled in the center of the head of the humerus or femur, perpendicular to the long axis of the limb. The frozen, straightened limb was then suspended on the device by fitting the hole in the head of the humerus or femur onto the end of the protruding bolt, which served as the rotation point of the device. That is, the centers of rotation of the limb and the metal pendulum were coincident. The limb was firmly secured to the metal pendulum using lightweight fishing line so that the entire assembly rotated as a unit. The swing period of the limb-metal pendulum combination was determined by measuring with a stopwatch the time for 10 small-amplitude oscillations of the system and dividing this value by 10. The swing was initiated by rotating the limb-metal pendulum assembly so that it made an angle of 15° with the vertical, and letting it fall. This was done three separate times and the results averaged to yield a value for the swing period of the limb-metal pendulum assembly (t_{l+mp}). The swing period (t_{mp}), mass (M_{mp}) and center-of-mass (CM_{mp}) had previously been measured for

the metal pendulum alone. These values had been used to calculate the moment-of-inertia of the metal pendulum about its point of rotation (I_{mp}), according to the equation for a compound (physical) pendulum (Tipler, '76):

$$I_{mp} = (t_{mp})^2 M_{mp} g CM_{mp}/4\pi^2, \quad (1)$$

where g is the acceleration due to gravity. The moment-of-inertia of the limb itself about the proximal end (I) was then calculated from the equation (Myers and Steudel, '85):

$$I = [(LM CM) + (M_{mp} CM_{mp})] g (t_{1+mp}/2\pi)^2 - I_{mp}, \quad (2)$$

where all variables are as previously defined. Limb radius of gyration about the proximal end (RG) was computed according to the equation (Kreighbaum and Barthels, '81):

$$RG = (I/LM)^{1/2}, \quad (3)$$

where all variables are as previously defined. The natural pendular period (NPP) of each limb was computed, modelling the limb as a compound pendulum, according to the equation (Tipler, '76):

$$NPP = (I 4\pi^2/LM CM g)^{1/2}, \quad (4)$$

where all variables are as previously defined.

Statistical analysis

Once all limb variables were measured, the mean value (across all dogs) was calculated for each variable. The hindlimb-forelimb difference in each measure was tested for significance using a paired t-test. Correlation coefficients were also computed for the relationship between forelimb and hindlimb values of each variable. Equations for estimating key limb parameters were developed using least-squares regression. All other regression analyses also used the method of least-squares.

RESULTS

Key measurements for each of our experimental animals are listed in Table 1. All limb data were taken on straightened limbs from the animal's right side. Table 2 compares forelimb and hindlimb values for a number of limb measures, showing the average differences (across all dogs) and the interlimb correlations. On average, hindlimbs have significantly greater total length (TL) (14%), limb mass (LM) (58%), and limb moment-of-inertia (I) (57%) than do forelimbs. Proximal segment length (PL), distal segment length (DL) and mid-joint circumference (MJC) are also larger in the hindlimb,

TABLE 2. Comparison of forelimb (FL) and hindlimb (HL) variables¹

| Variables | FL avg | HL avg | Avg HL- avg FL diff | % Inc avg HL over avg FL | Paired t-test signif. | FL vs HL corr. | Corr. signif. |
|---|-----------------|-------------------|---------------------------|--------------------------------|-----------------------------|-------------------|------------------|
| Limb mass (LM) (gm) | 655.7 (62.4) | 1032.9 (114.8) | 377.3 (59.1) | 58% | <.001 | .95 | <.0001 |
| Limb inertia (I) (gm-m ²) | 21.6 (3.9) | 33.9 (6.3) | 12.3 (2.5) | 57% | <.001 | .99 | <.0001 |
| Total limb length (TL) (cm) | 38.8 (2.0) | 44.1 (2.4) | 5.3 (0.5) | 14% | <.001 | .99 | <.0001 |
| Proximal segment length (PL) (cm) | 11.2 (0.6) | 14.7 (0.9) | 3.5 (0.7) | 31% | <.001 | .60 | .0385 |
| Midsegment length (ML) (cm) | 15.1 (1.3) | 12.6 (1.2) | -2.4 (0.5) | -16% | .001 | .91 | .0001 |
| Distal segment length (DL) (cm) | 12.6 (0.6) | 16.8 (0.9) | 4.2 (0.4) | 33% | <.001 | .92 | <.0001 |
| Proximal + midsegment length (PML) (cm) | 26.3 (1.4) | 27.3 (1.6) | 1.1 (0.5) | 4% | .036 | .96 | <.0001 |
| Mid + distal segment length (MDL) (cm) | 27.6 (1.8) | 29.4 (2.1) | 1.8 (0.6) | 6% | .010 | .97 | <.0001 |
| Midjoint circumference (MJC) (cm) | 13.4 (0.7) | 17.9 (0.6) | 4.6 (0.4) | 34% | <.001 | .87 | .0003 |
| Distal joint circumference (DJC) (cm) | 9.4 (0.3) | 9.1 (0.6) | -0.3 (0.5) | -3% | .535 | .58 | .0502 |
| Limb center of mass (CM) (cm) | 13.4 (0.9) | 13.4 (0.7) | 0.0 (0.3) | 0% | .939 | .94 | <.0001 |
| Radius of gyration (RG) (cm) | 17.1 (1.0) | 17.1 (0.9) | 0.0 (0.3) | 0% | .972 | .96 | <.0001 |
| Natural pendular period (NPP) (s) | 0.93 (0.03) | 0.93 (0.02) | 0.00 (0.01) | 0% | .894 | .97 | <.0001 |

¹Averages are computed across all dogs for the right forelimb or right hindlimb. Standard errors are in parentheses.

whereas the forelimb has a longer mid segment length (ML). There are marginal or nonsignificant differences in distal joint circumference (DJC), proximal plus midsegment length (PML), and mid plus distal segment length (MDL). Despite the noted differences, the average forelimb and hindlimb values for limb center-of-mass (CM), radius of gyration (RG) and natural pendular period (NPP) are indistinguishable (Table 2).

Although the coupling between hindlimb length and forelimb length is tight ($r = 0.99$), the least-squares regression line for this relationship is below the line of identity (i.e., our dogs' forelimbs are always shorter than their hindlimbs), and the divergence between forelimb and hindlimb length increases as TL gets larger (Fig. 3A). The regression lines relating fore- and hindlimb CM (Fig. 3B), RG (Fig. 3C), and NPP (Fig. 3D) are close to the line of identity and the correlation coefficients for the regressions are high ($r = 0.94$, $r = 0.96$ and $r = 0.97$, respectively). Thus, despite the forelimb-hindlimb TL differential, values for CM, RG, and NPP in the forelimb are quite similar to those in the hindlimb. Lemur (Wells and DeMenthon, '87) and rhesus monkey (Vilensky, '79) data, calculated for straightened limbs from information in the literature, were added to these graphs for comparison.

Figure 4A depicts the relationship between NPP and $TL^{1/2}$ with forelimb and hindlimb values combined. Although the least-squares regression is significant ($P < 0.0001$,

$r = 0.91$), there is a systematic difference between the forelimb and hindlimb points (all but one forelimb value is above the regression line, and all but one hindlimb value is below it) that is not accounted for by limb length. This extra variation is better explained when forelimb and hindlimb values are regressed separately (forelimb: $r = 0.95$, hindlimb: $r = 0.97$) on $TL^{1/2}$ (Fig. 4B).

Dog limb moment-of-inertia is closely related to limb length in both hindlimbs and forelimbs (Fig. 5; Table 3). In fact, the regression lines for the two types of limbs are quite similar. The predicted inertia for a given length of limb depends very little on whether the limb is a foreleg or a hindleg.

Table 3 presents regression equations for several functionally important forelimb and hindlimb variables which cannot be measured directly on living dogs. The equations allow these variables to be estimated from characteristics of intact animals.

DISCUSSION

Relationships among limb length, shape and other key variables

Limb measurements and predictive regression equations reveal systematic differences between the forelimbs and hindlimbs in mass (LM), moment-of-inertia (I), and total length (TL). However, these data show strong similarity between limbs in center-of-mass (CM), radius of gyration (RG), and natural pendular period (NPP) (Table 2; Fig. 3A–D).

As seen in Figure 2, both forelimbs and hindlimbs have shapes intermediate between a cone and a cylinder. To characterize the shape of dog limbs, and differences in shape between the fore- and hindlimbs, we compared the actual values of key limb variables to those of cone-shape or cylinder-shape limbs of the same mass and volume. For an ideal cone or cylinder, CM, RG, and NPP are systematically related to TL, for all but very low (i.e., 4:1 or less) length to radius ratios (see Appendix for derivation of these relationships). Table 4 lists the slopes of these relationships for an ideal cylinder, an ideal cone, the average dog forelimb, and the average dog hindlimb. For all three variables (CM, RG, and NPP), the constants for both forelimbs and hindlimbs are between those for the cone and for the cylinder. However, these measures show that hindlimbs are consistently more conical than forelimbs, which tend to be more cylindrical in shape (Fig. 6A–B). This relationship means that CM, RG, and NPP all increase at a

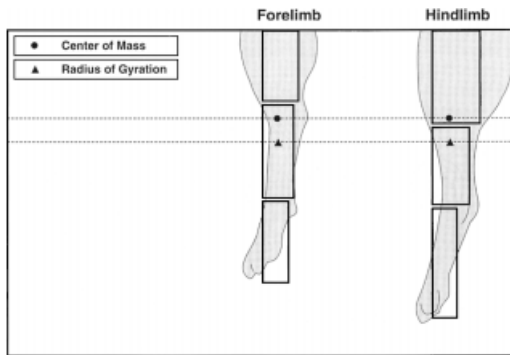


Fig. 2. *Canis familiaris*. Schematic representation of average (across all 12 dogs) dog forelimb and hindlimb. Outline of representative forelimb and hindlimb is superimposed for comparison with idealized limbs. Positions of total limb center-of-mass (filled circles) and radius of gyration (filled triangles) are shown. Proximal segment diameter = MJC/π ; midsegment diameter = $(MJC + DJC)/2\pi$; distal segment diameter = DJC/π .

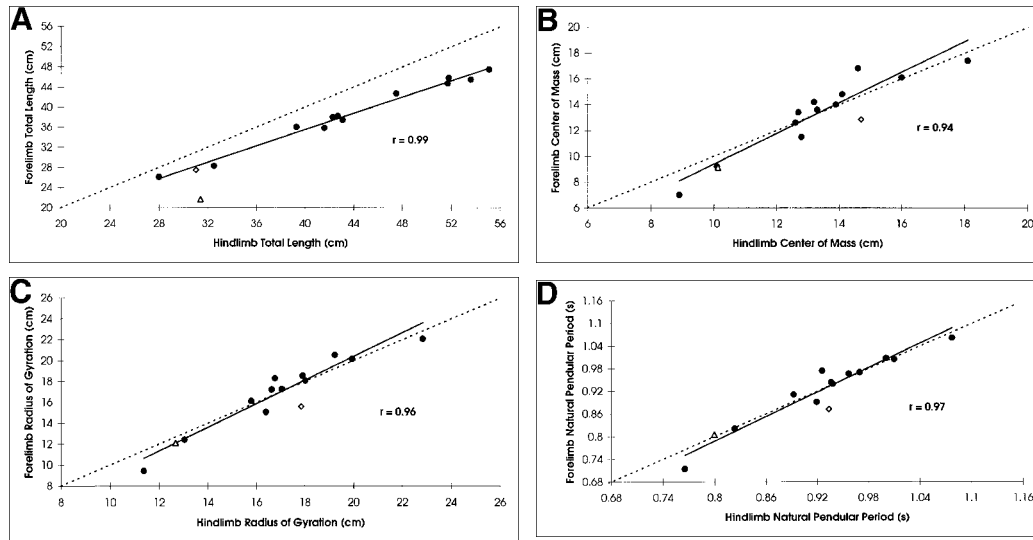


Fig. 3. *Canis familiaris*. Forelimb vs. hindlimb values for: **A**, total limb length ($R^2 = 0.99$, Intercept (SE) = 3.16 (1.40), Slope (SE) = 0.81 (0.03), $P < 0.00001$), **B**, limb center-of-mass ($R^2 = 0.89$, Intercept (SE) = -2.44 (1.81), Slope (SE) = 1.18 (0.13), $P < 0.00001$), **C**, radius of gyration ($R^2 = 0.93$, Intercept (SE) = -2.22 (1.73), Slope (SE) = 1.13 (0.10), $P < 0.00001$), and **D**, natural pendular period ($R^2 = 0.94$, Intercept (SE) = -0.08

(0.08), Slope (SE) = 1.08 (0.09), $P < 0.00001$). The dotted line represents identity (forelimb value equal to the hindlimb value). Values from the literature are also given for a lemur (*Lemur fulvus*) (open triangles: Wells and DeMenthon, '87) and for a sample of rhesus monkeys (*Macaca mulatta*) (open diamonds: Vilensky, '79).

faster rate with increasing TL in the forelimb than in the hindlimb.

Because a real limb is irregular in shape and does not have constant density, its center-of-mass, radius of gyration, and natural pendular period depend on both its length and its shape (mass distribution). This is why, for instance, dog limb NPP varies with $TL^{1/2}$ in a different manner in the forelimb than in the hindlimb (Fig. 4B).

The most interesting fact about the shape difference between the fore- and hindlimbs is that it largely compensates for the effect of the observed length disparity (Fig. 3A) on NPP (Fig. 3D). That is, forelimbs are shorter than hindlimbs, which by itself would mean lower forelimb NPP. However, forelimbs are also more cylindrical, which adds more to forelimb NPP than to hindlimb NPP. The net result is that the forelimbs and hindlimbs of the dogs in our sample have very similar natural pendular periods of oscillation.

If equation (3) is substituted into equation (4), it can be seen that the term $RG/(CM)^{1/2}$ must be the same in both forelimbs and hindlimbs if NPP is to match. Although this could be achieved without RG and CM being the same, the forelimbs and hindlimbs of the

dogs in our study have remarkably similar RG and CM. However, the correlation between fore- and hindlimb NPP is the tightest of the three variables (Fig. 3) and appears to drive the observed correlations for RG and CM.

The relationship between limb moment-of-inertia and limb length is quite good for both the forelimb and the hindlimb (Fig. 5; Table 3). If animals scale according to geometrical similarity (lengths \propto diameters), then I should be proportional to TL^5 ($I \propto \text{mass} * \text{length}^2 \propto \text{length} * \text{diameter}^2 * \text{length}^2 \propto \text{length}^5$). In both birds (Kirkpatrick, '90) and bats (Thollesson and Norberg, '91), total wing moment-of-inertia has been found to scale very close to (wing span) 5 . Human forearm inertia, over a fourfold range in length, was shown to correlate well ($r = 0.84$) with (forearm length) 5 (Walsh and Wright, '87). In our dog sample, both forelimb and hindlimb I is highly correlated with TL^5 ($r = 0.99$). However, the slopes of the log I on log TL regressions are 3.8 and 3.5, for the forelimb and hindlimb respectively. Both slopes are significantly different from 5 ($P < 0.5$). This deviation from geometrical similarity in the scaling of limb I is the consequence of limb

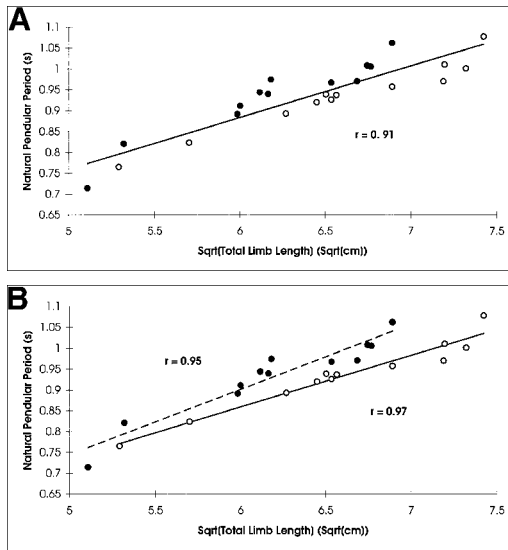


Fig. 4. *Canis familiaris*. **A.** Natural pendular period vs. (total limb length)^{1/2} for all 12 dogs. Regression line ($R^2 = 0.82$, Intercept (SE) = 0.14 (0.08), Slope (SE) = 0.12 (0.01), $P < 0.00001$) is for forelimb (filled circles) and hindlimb (open circles) values combined. **B.** Natural pendular period vs. (total limb length)^{1/2} for all 12 dogs. Dashed regression line ($R^2 = 0.91$, Intercept (SE) = -0.04 (0.10), Slope (SE) = 0.16 (0.02), $P < 0.00001$) is for forelimb values (filled circles) and solid regression line ($R^2 = 0.94$, Intercept (SE) = 0.12 (0.06), Slope (SE) = 0.12 (0.01), $P < 0.00001$) is for hindlimb values (open circles).

diameters not increasing proportionally to limb lengths, and therefore limb mass not increasing in proportion to limb length³. That is, in our dog sample, limbs are longer relative to their diameters, and less massive, as limb length increases.

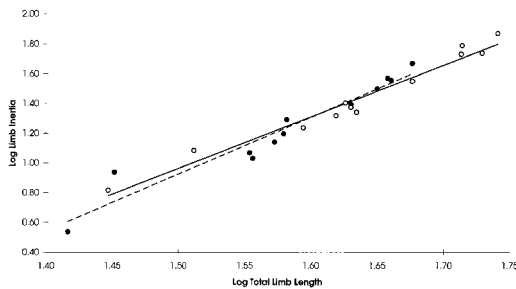


Fig. 5. *Canis familiaris*. Log limb inertia vs. log total limb length for all 12 dogs. Dashed regression line ($R^2 = 0.94$, Intercept (SE) = -4.82 (0.51), Slope (SE) = 3.83 (0.32), $P < 0.00001$) is for forelimb values (filled circles) and solid regression line ($R^2 = 0.97$, Intercept (SE) = -4.24 (0.34), Slope (SE) = 3.47 (0.21), $P < 0.00001$) is for hindlimb values (open circles).

The similarity between hindlimbs and forelimbs in the log TL-log I relationship is of interest. It results from the previously noted systematic differences between fore- and hindlimbs in mass and distribution of mass. For a given length, hindlimbs are more massive than forelimbs (due to their greater average diameters), but forelimbs have a greater radius of gyration than hindlimbs (because they are more cylindrical). Because I is the product of LM and RG^2 , the effects of these opposing influences are largely canceled, yielding a fairly robust relationship between limb length and moment-of-inertia.

Estimated forelimb and hindlimb NPP in mammals across a large size range

As noted above, the NPP of dog forelimbs and hindlimbs is very similar, apparently because differences in shape counterbalance differences in length. Does this situation occur in other species? We attempted to answer this question by estimating NPP in mammals across a large size range. In a study on the scaling of cursoriality in mammals, Steudel and Beattie ('93) reported limb length data they collected on 64 mammalian species, combined with data from 114 species of bovids (Scott, '79). We used limb length data from this combined dataset, for mammals ranging in size from ~0.1 kg to almost 1,000 kg, to estimate limb NPP.

Figure 7A shows a forelimb length-hindlimb length relationship in mammals that is very similar to the pattern seen in dogs (Fig. 3A), i.e., forelimbs significantly shorter than hindlimbs. If the forelimbs and hindlimbs of this group of mammals do not differ in shape, then forelimb NPP should be consistently lower than hindlimb NPP. Given that mammals are generally geometrically similar (i.e., retain a constant shape) across large ranges of size (Alexander et al., '79; Raich and Casinos, '91; Prothero, '92), we made the assumption that the shape differences we have characterized in dog forelimbs and hindlimbs would be generally observed across all mammals. Thus we estimated NPP in two ways: (1) we determined limb CM, using the forelimb and hindlimb CM vs. TL slopes in Table 4 and then calculated NPP as the period of a simple pendulum, $2\pi(CM/g)^{1/2}$, with length equal to limb CM, and (2) we computed NPP directly using the forelimb and hindlimb NPP vs. TL^{1/2} slopes in Table 4. Although the actual NPP values produced by the two meth-

TABLE 3. Regression equations for key forelimb (FL) and hindlimb (HL) variables¹

| Variables | Limb | Regression equations | r | SE of est | SE of slope |
|---------------------------------------|------|---------------------------------------|------|-----------|-------------|
| Limb mass (LM) (gm) | FL | $\log LM = 1.539 + 1.049(\log BM)$ | 0.92 | 0.057 | 0.136 |
| | HL | $\log LM = 0.529 + 1.720(\log PML)$ | 0.94 | 0.058 | 0.191 |
| Limb inertia (I) (gm-m ²) | FL | $\log I = -4.821 + 3.830(\log TL)$ | 0.97 | 0.087 | 0.319 |
| | HL | $\log I = -4.241 + 3.469(\log TL)$ | 0.98 | 0.061 | 0.206 |
| Limb center of mass (CM) (cm) | FL | $\log CM = -0.201 + 0.921(\log MDL)$ | 0.98 | 0.023 | 0.058 |
| | HL | $\log CM = -0.322 + 0.880(\log TL)$ | 0.96 | 0.023 | 0.079 |
| Radius of gyration (RG) (cm) | FL | $\log RG = 0.035 + 0.832(\log MDL)$ | 0.98 | 0.021 | 0.054 |
| | HL | $\log RG = -0.208 + 0.876(\log TL)$ | 0.97 | 0.019 | 0.065 |
| Natural pendular period (NPP) (s) | FL | $\log NPP = -0.563 + 0.372(\log MDL)$ | 0.97 | 0.011 | 0.027 |
| | HL | $\log NPP = -0.744 + 0.436(\log TL)$ | 0.98 | 0.009 | 0.030 |

¹In each case, the reported regression equation is that which had the largest correlation coefficient. All regressions are significant at the $P < .0001$ level. Units are: BM (kg), TL (cm), PML (cm), and MDL (cm).

ods differ systematically (the simple pendulum method always underestimates directly measured NPP) (Myers et al., '96), the forelimb vs. hindlimb comparison of both estimates yields the same results, namely, that forelimb and hindlimb estimated NPP is quite similar across a large size range of mammals (Fig. 7B, slope of regression line is not significantly different from 1 at $P = 0.05$). Thus the convergence of fore- and hindlimb NPP observed in dogs may be a more general phenomenon in mammals. Without more detailed information on limb shape, it is not possible to determine just how well the NPP of the forelimbs and hindlimbs matches in any particular species.

Limb NPP for other species calculated from segment inertia data

We were able to estimate total limb NPP for a lemur and a sample of rhesus monkeys from segment inertia data in the literature (lemur: Wells and DeMenthon, '87; rhesus monkeys: Vilensky, '79), as both sources contained information on segment length, moment-of-inertia and the absolute distance from the proximal joint to the center-of-mass. Several other references on segment inertia did not report enough information to

allow total limb parameters to be calculated (e.g., Fedak et al., '82; Jayes and Alexander, '82; Hoy and Zernicke, '85). We did not use the well-known cat segment inertia data of Manter ('38) because the segment length and center-of-mass values yielded a total limb radius of gyration that was smaller than the distance to the center-of-mass, which is a physical impossibility (Tipler, '76).

The lemur, whose hindlimbs are much longer (45%) than its forelimbs (Fig. 3A), has

TABLE 4. Slopes of CM vs. TL, RG vs. TL, and NPP vs. (TL)^{1/2} for an ideal cylinder, an ideal cone, the average dog forelimb, and the average dog hindlimb¹

| | Slope of CM vs. TL | Slope of RG vs. TL | Slope of NPP vs. (TL) ^{1/2} |
|----------------------|--------------------|--------------------|--------------------------------------|
| Ideal cylinder | 0.50 | 0.58 | 0.16 |
| Ideal cone | 0.25 | 0.32 | 0.13 |
| Average dog forelimb | 0.35 | 0.44 | 0.15 |
| Average dog hindlimb | 0.30 | 0.39 | 0.14 |

¹Constants are valid for biologically reasonable limb length to diameter ratios. Units for the NPP vs (TL)^{1/2} slope are s/(cm)^{1/2}.

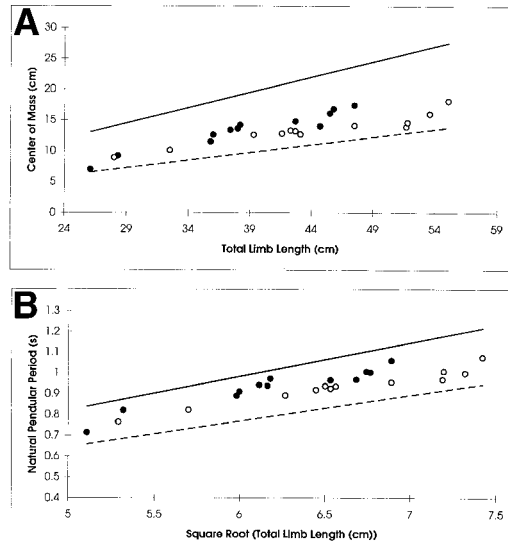


Fig. 6. *Canis familiaris*. **A.** Limb center-of-mass vs. total limb length for an ideal cylinder (solid line), an ideal cone (dashed line), actual forelimb values (filled circles), and actual hindlimb values (open circles). **B.** Natural pendular period vs. (total limb length)^{1/2} for an ideal cylinder (solid line), an ideal cone (dashed line), actual forelimb values (filled circles), and actual hindlimb values (open circles).

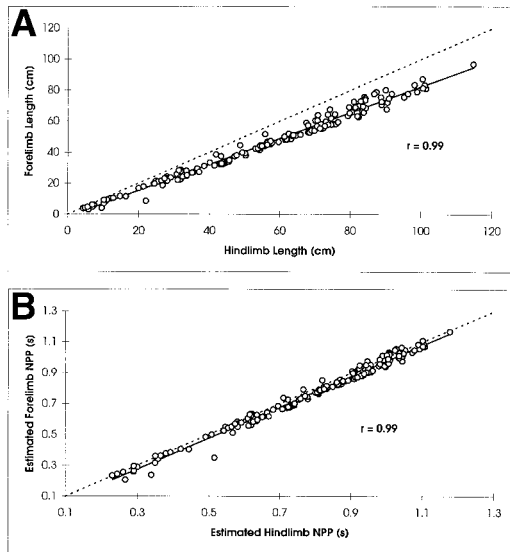


Fig. 7. From mammals across a large size range, forelimb vs. hindlimb values for: **A**, total limb length ($R^2 = 0.99$, Intercept (SE) = -1.40 (0.47), Slope (SE) = 0.84 (0.01), $P < 0.00001$), and **B**, estimated natural pendular period ($R^2 = 0.99$, Intercept (SE) = -0.02 (0.01), Slope (SE) = 1.00 (0.01), $P < 0.00001$). The dotted line represents identity (forelimb value equal to the hindlimb value). Limb length data were taken from Steudel and Beattie ('93). Natural pendular period estimates were calculated using actual limb lengths in combination with constants derived from the dog sample (see text for details).

almost identical forelimb and hindlimb NPP (Fig. 3D), owing to the distinct difference in shape between its limbs (forelimb CM is 42% of TL; hindlimb CM is 32% of TL). As the position of the CM in the hindlimb is within the range observed in our dog sample, it appears that it is the unusually cylindrical forelimb (compared to dogs) that accounts for NPP matching so closely in the lemur. Rhesus monkeys have shorter forelimbs than hindlimbs, but the length difference is much the same as in dogs (Fig. 3A). However, rhesus forelimbs and hindlimbs are similar in shape, and both are considerably more cylindrical than dog forelimbs (CM is 47% of TL in both fore- and hindlimbs). Because, in this case, differences in shape do not mitigate length differences, hindlimb NPP is $\sim 7\%$ higher than forelimb NPP in rhesus monkeys (Fig. 3D). A comparison of the limbs of these two species provides another illustration of the influence of limb shape (mass distribution) per se on NPP; rhesus monkeys and the lemur have virtually identical

hindlimb lengths, yet rhesus monkeys have 17% higher hindlimb NPP than does the lemur because their hindlimbs are extremely cylindrical in shape.

Influence of limb flexion on NPP

We measured all limb values on straightened limbs, because this is an easily replicated standardized configuration that represents the upper boundary for all limb length-related variables. The degree of flexion of an animal's limb changes throughout a stride, so the effective NPP of the limb will be somewhere between that for the straightened limb and the fully flexed limb. To assess whether the effective NPP of fore- and hindlimbs is as similar as that of straightened limbs, we need to know: (1) how much the NPP of a limb differs between the straightened and the fully flexed orientation, and (2) how similar the extent of flexion is in the forelimb and hindlimb during the swing phase.

To address the first of these questions, we estimated the position of the limb CM for a dog forelimb when straightened and when in the most flexed orientation used during walking (Fig. 8) (limb orientation angles taken from Goslow et al., '81; limb CM calculated using segment lengths, masses and CM's from Dog #1). Limb CM is 13% lower in the flexed orientation, whereas limb I, estimated using the simple pendulum method, is decreased 25% (when mass is constant, $I \propto \text{length}^2$). Limb NPP is only reduced 7% by limb flexion (when mass is constant, $\text{NPP} \propto \text{length}^{1/2} \propto I^{1/4}$). These findings agree with Hildebrand's ('85) observation that limb center-of-mass for most walkers is changed very little by limb flexion. With respect to the second question, flexion in forelimbs and hindlimbs during the swing phase of walking is quite similar in both amount and duration (Arshavskii et al., '65; Goslow et al., '81). This is especially true for the joint between the proximal and distal segments ("elbow" or "knee"), which accounts for most of the change in the position of the limb CM. This postural symmetry is not as true for human upper and lower limbs, as the upper limbs flex very little during walking. The flexion of the lower limbs causes a slightly reduced (from the straightened limb) NPP, bringing them within 12% of the NPP of the upper limbs (Witte et al., '91).

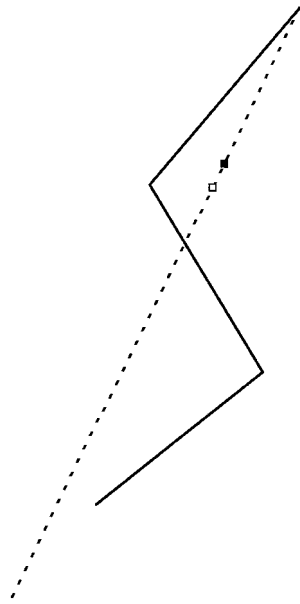


Fig. 8. *Canis familiaris*. Center-of-mass position of the entire limb calculated for the straightened limb (dotted line, open square) and the fully flexed limb (solid line, filled square). Mass, center-of-mass, and length data used in these calculations were taken from Dog #1. Limb position data were taken from Goslow et al. ('81) for a similar size dog.

Evidence that limb NPP is linked to walking swing period

We argue here that to maximize the pendular exchange of energy within limbs, fore- and hindlimb NPP should be similar because the observed swing times for all four limbs is similar. However, this reasoning presumes that animals actually spend a significant fraction of time oscillating their limbs with swing periods that are close to their limb NPP. There is evidence that walking humans and animals tend to use limb swing periods close to, or proportional to, limb NPP (Mochon and McMahon, '80; Hildebrand, '85; Turvey et al., '88; Holt et al., '91; Witte et al., '91). Hildebrand ('85) suggests that a nontrivial amount of energy can be saved by pendular exchange even in some trots and slow gallops, where limbs need to swing somewhat faster than their NPP. In addition, two lines of evidence related to limb shape support the link between limb NPP and swing duration.

If the shape, or mass distribution, of a limb is altered, then limb NPP will change accordingly. This in turn should change the

target swing period, and likely the stride period, of the walking animal so that resonance is maintained. This is indeed what is seen in experiments in which limb "shape" is changed by the addition of mass to the limbs. Steudel ('90b) added loads (3–4% of body mass) to dog limbs in such a way that limb CM was increased (i.e., limbs became more "cylindrical"), and thus so was limb NPP. Limb-loaded dogs showed a small but significant ($P < 0.05$) reduction in stride frequency (increase in stride period). The drop in stride frequency was most pronounced at the lowest speed (walk) and became less so as speed increased. This was as expected as the extent to which the pendular mechanism operates decreases with speed (Hildebrand, '85). Similar results have been observed in limb-loaded walking humans (Russell and Belding, '46; Inman et al., '81).

Webb and co-workers ('94) report that as humans increase their speed of walking, from very slow and slow speeds to normal and fast speeds, they change from "double swinging" both upper limbs in unison, at twice the frequency of the lower limbs, to "single swinging" their arms, in phase with the contralateral lower limb. These authors found that the transition between double and single swinging occurs at or slightly below the natural pendular frequency of the upper limbs, as a result of entrainment (2:1 and 1:1) of the upper arms (modelled as compound pendulums) to the movements of the lower limbs. When hand weights were added to reduce the natural pendular frequency of the upper limbs, there was a parallel decrease in the frequency at which the switch from double to single swinging occurred.

Another example of the connection among limb shape, limb NPP, and stride period is seen in ungulates. This group of animals does not have unusually long limbs, but does have a relatively high metatarsal/femur ratio (Steudel and Beattie, '93) and thus more conical limbs than other animals of the same limb length. This suggests that their limb NPP should be relatively short and that they should use unusually short stride periods. Indeed, Alexander and Jayes ('83) found that "cursorial" mammals (which includes ungulates) have shorter relative stride periods than their "non-cursorial" counterparts.

Locomotor consequences of limb length and shape

In what ways do limb length and shape influence locomotor energetics? Limb length

is an important determinant of limb NPP; limb shape plays a pivotal role in modulating this relationship. Limb length also contributes to limb mass, and both limb length and shape determine the distance between the proximal joint and the limb center-of-mass. Both of these terms strongly influence limb moment-of-inertia, which scales as limb length⁵ in geometrically similar animals. These morphological parameters, in combination with limb kinematics, determine the rotational and translational kinetic energy of the limbs during locomotion. Thus a fairly small increase in limb length can significantly elevate the mechanical energy of the oscillating limbs (Swartz, '89; Witte et al., '91), especially at speeds where pendular exchange of energy within limbs is minimal. On the other side of the equation, at a given speed, longer limbs mean that NPP (assuming constant shape), stride period and stride length will all increase in proportion to limb length^{1/2} (Witte et al., '91). Relatively long, slow strides should decrease both the internal work of moving the limbs (e.g., Minetti and Saibene, '92), and the cost of producing muscular force, due to relatively slow muscle contraction rates (Kram and Taylor, '90). It seems reasonable that limb lengths observed in animals reflect the point at which these contrary energetic effects are balanced (Steu-del, '96). In geometrically similar animals, limb NPP should scale as limb I^{1/10} (NPP \propto length^{1/2}, I \propto length⁵). Thus, NPP is relatively insensitive to changes in I, and a given change in limb length will influence I much more dramatically than NPP.

Our data suggest that the balance point for these competing energetic constraints is different in the forelimb than in the hindlimb. The more distal distribution of limb mass in forelimbs is not consistent with minimization of limb CM and I. Instead, forelimbs are uniformly more cylindrical than hindlimbs, to the extent required for their NPP to approach that of hindlimbs. Hindlimbs, however, exhibit a consistently more proximal distribution of mass. Because dog hindlimbs are more massive than forelimbs, it is energetically preferable to have hindlimbs shaped to minimize I and CM (to minimize the amount of energy provided by muscular contraction), and forelimbs shaped to equalize NPP (to maximize the amount of energy saved by pendular exchange). This idea is supported by the finding that heavier hindlimbs are significantly more conical than

lighter hindlimbs, while there is no correlation between limb mass and limb shape in forelimbs.

It is possible that the forelimb-hindlimb matches in NPP that we observe in our dog sample and estimate in other species are merely the secondary result of evolutionary shaping by other locomotor constraints (e.g., optimal muscular and skeletal development for generating forces or resisting locomotor stresses). As discussed above, we believe the energetic consequences of limb NPP interact with other locomotor functions to constrain the morphology of limbs; the result being a finely-tuned coadapted system. In this study, numerous examples have been presented in which limb shape has almost exactly compensated for differences in length to yield limbs with closely similar natural pendular periods; the most dramatic case being the lemur in which a 45% difference in length has been counterbalanced by an unusually cylindrical forelimb shape. Based on this evidence, we believe the conservation of limb NPP within an animal is due to adaptive pressure that results from the attendant energetic advantages and is not merely a serendipitous outcome.

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APPENDIX

The sections below describe the relationships between center-of-mass (CM), radius of gyration (RG), and natural pendular period (NPP) for an ideal solid cone and cylinder of constant density. In the following equations, M is the mass of the solid, L is the length of the solid, R is the radius of the solid, I is the moment-of-inertia about an axis through either end in the cylinder and through the base in the cone, g is the acceleration due to gravity, and c is the ratio of the length of the solid to its radius (L/R).

Relationship between CM and TL

For a cylinder, the center-of-mass along the long axis is located halfway between the two ends (by symmetry). Thus, $CM = 0.5 L$ for any cylinder.

For a cone, the center-of-mass along the long axis is located a distance from the base equal to $\frac{1}{4}$ the total length of the cone (by integration). Thus, $CM = 0.25 L$ for any cone.

Relationship between RG and TL

For a cylinder (Tipler, '76),

$$\begin{aligned} RG &= (I/M)^{1/2} \\ &= [M((L^2/3) + (R^2/4))/M]^{1/2} \\ &= [(L^2/3) + (R^2/4)]^{1/2} \end{aligned} \quad (5)$$

In order to simplify the equation, L/c can be substituted for R to yield,

$$RG = L[4c^2 + 3]/12c^2]^{1/2} \quad (6)$$

For very small length to radius ratios (very small c), RG approaches infinity. For reasonably large length to radius ratios (reasonably large c), RG approaches $0.58 L$.

For a cone (Tipler, '76),

$$\begin{aligned} RG &= (I/M)^{1/2} \\ &= [(M/20)(2L^2 + 3R^2)/M]^{1/2} \\ &= [(1/20)(2L^2 + 3R^2)]^{1/2} \end{aligned} \quad (7)$$

In order to simplify the equation, L/c can be substituted for R to yield,

$$RG = L[(2c^2 + 3)/20c^2]^{1/2} \quad (8)$$

For very small length to radius ratios (very small c), RG approaches infinity. For reasonably large length to radius ratios (reasonably large c), RG approaches $0.32 L$.

Relationship between NPP and TL

For a cylinder (Tipler, '76),

$$\begin{aligned} NPP &= 2\pi(I/MgCM)^{1/2} \\ &= 2\pi[M((L^2/3) + (R^2/4))/MgCM]^{1/2} \\ &= 2\pi(2/g)^{1/2}[(L^2/3) + (R^2/4)]^{1/2} \end{aligned} \quad (9)$$

In order to simplify the equation, L/c can be substituted for R , 981 cm/s^2 substituted for g , and $L/2$ substituted for CM to yield,

$$NPP = 0.28L(4c^2 + 3)/12c^2]^{1/2} \quad (10)$$

For very small length to radius ratios (very small c), NPP approaches infinity. For reasonably large length to radius ratios (reasonably large c), NPP approaches $0.16 L^{1/2}$ (where L is in cm).

For a cone (Tipler, '76),

$$\begin{aligned} NPP &= 2\pi[I/MgCM]^{1/2} \\ &= 2\pi[(M/20)(2L^2 + 3R^2)/MgCM]^{1/2} \\ &= [2\pi/(5g)^{1/2}][(2L^2 + 3R^2)/L]^{1/2} \end{aligned} \quad (11)$$

In order to simplify the equation, L/c can be substituted for R , 981 cm/s^2 substituted for g , and $L/4$ substituted for CM to yield,

$$NPP = 0.09[L(2c^2 + 3)/c^2]^{1/2} \quad (12)$$

For very small length to radius ratios (very small c), NPP approaches infinity. For reasonably large length to radius ratios (reasonably large c), NPP approaches $0.13 L^{1/2}$ (where L is in cm).