TIME OF CONTACT AND STEP LENGTH: THE EFFECT OF LIMB LENGTH, RUNNING SPEED, LOAD CARRYING AND INCLINE

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Summary

Using published values for twelve species of birds and mammals, we investigated the effects of limb length and running speed on time of contact and step length. In addition, we measured the time of contact in horses trotting up a 10 % incline and when carrying a load averaging 19 % of their body mass. From these values, we calculated stride period and step length. Our analysis of the interspecific data yielded the following relationship between time of contact (t_c in s) and leg length (L in m) and running speed (v in m s^{-1}): $t_c = 0.80L^{0.84}/v^{0.87}$ ($r^2 = 0.97$). Both exponents in this relationship are significantly different from 1.0, indicating that step length increases with speed and that small species use a step length that, relative to their leg length, is longer than the relative step length used by larger species. Time of contact increased when a horse carried a load but not when it trotted up an incline.

Key words: locomotion, time of contact, step length, scaling, leg length, horse.

Introduction

The duration of the stance phase of the stride (time of contact, t_c) explains most of the speed-related and size-related differences in the metabolic cost of locomotion (Kram and Taylor, 1990; Roberts et al., 1998). When locomoting, all the force necessary to support an animal's body weight must be generated during the period that the foot is in contact with the ground (t_c). The rate at which this force must be applied is inversely proportional to t_c. Kram and Taylor (1990) showed that the rate of force application (t_c^{-1}) is a linear function of speed in five species of terrestrial mammals and that the slope of this relationship varies as a function of body mass just as does metabolic rate. This is convincing evidence that the metabolic cost of locomotion is largely determined by the rate at which force must be generated by the muscles that support the body during the stance phase. Roberts et al. (1998) reported very similar results in six species of biped.

In his detailed analysis of the relationship between the mechanics and energetics of locomotion, Taylor (1994) made the simplifying assumption that step length (the distance the body travels during the stance phase) was independent of speed and suggested that this would minimize energy cost by maintaining a constant average mechanical advantage. In quadrupeds, it was reported that 'step length increased only slightly' (Kram and Taylor, 1990) and in bipeds that 'step length changes little with speed' (Roberts et al., 1998). However, Gatesy and Biewener (1991) reported that step length increased with speed in seven species of avian biped and that small bipeds ran with relatively longer step lengths than did large bipeds.

We realized that for step length ($l_c = t_c \times v$, where v is speed) to remain the same at all speeds, time of contact would have to be inversely proportional to running speed ($t_c \propto v^{-1.0}$). While the studies of Kram and Taylor (1990) and Roberts et al., (1998) had reported the relationship between running speed and $1/t_c$, we wondered what the relationship was between t_c and running speed: how close was the exponent to -1.0? We therefore fitted power functions to their data and to our data for trotting horses.

In the present study, we attempt to develop a better understanding of time of contact because of its critical role in determining the cost of locomotion. We quantify the relationship between running speed and time of contact, so that we can determine whether step length is constant, as Taylor (1994) hypothesized, or whether it varies in a regular manner with speed. We also quantify the relationship between time of contact and leg length as a means of exploring the scaling of step length. Finally, we study the effects of load-carrying and trotting up an incline in horses to determine whether time of contact and step length are adjusted in a manner that conserves energy.

Materials and methods

Animals and experimental protocol

Five Arabian horses (three mares and two geldings) with a

mean body mass of 450±16 kg were trained on a treadmill (SATO-I) under three conditions: (1) on the level with no load; (2) on the level carrying a load equal to approximately 19 % of body mass; and (3) up a 10 % incline (with no load). Training lasted for 2–14 months and involved an average of four 30 min sessions per week. The load consisted of six bags of lead shot that were firmly attached to a standard horse saddle (total mass 85 kg) and, for the five animals, it averaged 19±0.6 % of their body mass. This mass was selected because we wished to elicit as large a response as possible without excessively stressing the animals, and this mass, which is similar to that of a typical rider and equipment, is one that the animals are accustomed to carrying. The saddle maintained a normal equine weight distribution of 60 % on the forelimbs and 40 % on the hind limbs. The 10 % incline was the maximum incline available on our treadmill and is one regularly used in exercising horses.

All data from an individual animal were obtained on a single day during the course of a study of muscle function in which sonomicrometry crystals were implanted in the vastus lateralis and biceps femoris muscles of the right hind limb. The horses were allowed to recover for approximately 90 min following the surgery and were evaluated for lameness or altered gait prior to the collection of data. Normal locomotory performance was also confirmed on the treadmill by comparing stride frequencies for each animal with data collected prior to surgery. After a brief warm-up, the animal trotted at each experimental speed for 45 s before the 15 s period of data collection began. The animal was then given a rest of approximately 2.5 min. The speeds used were 2.0, 2.5, 3.0, 3.5 and 4.0 m s^{-1}, and their order was randomized. After completing all the speeds under one experimental condition (level, load or incline), the animal was allowed to rest for approximately 1 h before starting the next experimental condition. The sequence of experimental conditions was varied systematically between the animals.

Experimental apparatus

The stride temporal parameters, time of contact (t_c) and duration of the swing phase (t_{sw}), were determined using a biaxial accelerometer (CXL25M2, Crossbow Technology, Inc.) firmly attached to the right hind hoof with double-sided tape and secured with additional elastic tape. The signal from the accelerometer was sampled at 4 kHz with an A/D card (PCI 1200, National Instruments) using LabVIEW software (National Instruments). The accelerometer signal (Fig. 1) was interpreted by comparison with video recordings obtained at 125 Hz using a high-speed digital camera (PCI 250, Redlake Imaging Corp.). The accelerometer recordings were remarkably consistent in different animals at different speeds and conditions.

The lengths of limb bones were measured on the lateral side of the right hind leg on four of the five horses used in this study while they were standing normally (the fifth horse was no longer available when we made these measurements). The lengths were measured using the following palpable markers: (1) femur, from the caudal aspect of the major trochanter to the
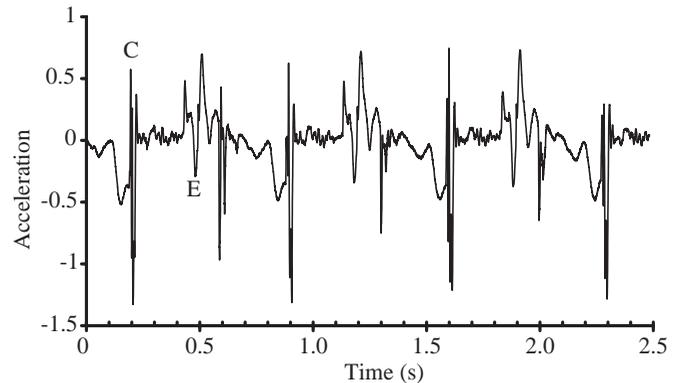

Fig. 1. A representative accelerometer recording showing the very pronounced waveform resulting from hoof contact with the tread (C) and the smaller waveform indicating the end of contact when the hoof leaves the tread (E). The recording shows acceleration in the direction parallel to the longitudinal axis of the animal's body when the hoof is on the tread, but the orientation changes throughout the remainder of the stride because the orientation of the hoof changes. The accelerometer is not calibrated, so the units of acceleration are not specified.

distal portion of lateral condyle; (2) tibia, from the proximal aspect of the lateral condyle to the distal aspect of the lateral malleolus; (3) third metatarsal, from the proximal aspect of the third metatarsal to its distal end; and (4) total phalangeal length from the proximal end of the first phalange to the distal hoof wall midway along its length. The values obtained were (mean ± S.D., N=4): femur, 40±1.6 cm; tibia, 42±2.3 cm; third metatarsal, 37±1.7 cm; total phalangeal length, 15.8±0.4 cm. The mean total length of the femur, tibia and metatarsal was 119.0±2.7 cm.

Published data on time of contact (t_c) in bipeds and quadrupeds

Data were obtained from two published graphs of $1/t_c$ *versus* speed (Kram and Taylor, 1990; Roberts et al., 1998). These data were used to calculate t_c and step length l_c. Leg lengths (L, the sum of the lengths of the femur, tibia and metatarsal) for all quadrupeds and most bipeds were estimated using the allometric equations of Roberts et al. (1998). The exceptions were the mammalian bipeds for which neither the biped nor quadruped allometric predictions seemed likely to be reliable (Roberts et al., 1998). For humans, published values were available for the femur and tibia, but the length of the metatarsals was included in the length of the foot (Gatesy and Biewener, 1991). We assumed that the length of the metatarsals was equal to half of the length of the whole foot and added this value to the lengths of the femur and tibia. The resulting value (1.003 m) differs by only 3 % from the average (1.034 m) of the allometrically predicted values for a biped and a quadruped of the same mass (1.384 m, 0.684 m, respectively). The leg length (0.059 m) of the same species of kangaroo rat (Steudel and Beattie, 1993) was only 1 % different from the average (0.060 m) of the allometrically predicted values for a

biped and quadruped (0.066 m and 0.053 m, respectively). We could find no published value for the spring hare, so we used the average of the allometric predictions for a biped and a quadruped. Our value for the leg length of the horse was the same as the allometric prediction (1.19 m).

Statistical analyses

For our data on horses, parametric statistical analyses were performed using the Macintosh computer programs SuperANOVA and Statview on untransformed data. For each animal, ten strides were averaged at each speed and condition. These mean values were then subjected to a repeated-measures analysis of variance (ANOVA) with two within-factors (condition and speed). When tests of sphericity using the Mauchly criterion were significant, Huynh–Feldt epsilons were used to adjust the degrees of freedom for the *F*-test. Mean separations were accomplished where significance existed using appropriately designed contrasts. Non-linearity was observed in the relationship between speed and the duration of the swing phase. For each condition, a regression analysis was performed using animal as a blocking variable to determine the linear and quadratic components for a polynomial equation. Each regression coefficient was tested to determine whether it was significantly different from zero. The data on time of contact in bipeds and quadrupeds were analyzed using least-squares regression analysis on log-transformed data. The slopes and intercepts of these regressions were evaluated using Student's *t*-tests.

The stride frequencies obtained in this study were validated by comparing them with control values obtained by measuring the time required for 20 strides with a stopwatch. The values measured on two animals climbing an incline at speeds of 3.5 and 4.0 m s^{-1} differed greatly from the control values; therefore, all the data from these animals at these speeds were removed from the analysis. Because of the resulting unequal sample sizes, these data were analyzed with a univariate repeated-measures ANOVA.

Results

Horse experiments

Time of contact (Fig. 2A) averaged 7.7 % longer (*P*=0.006) when a horse was carrying a load than when it was trotting on the level, but was not significantly different when it was trotting up an incline (*P*=0.434). Time of contact (t_c, with units of s) was a power function of trotting speed (*v*, with units of m s^{-1}) under all three conditions. The equations (based on mean values) describing these relationships are:

$$\text{Level: } t_c = 0.63v^{-0.680} \ (r^2 = 0.996), \tag{1}$$

$$\text{Load: } t_c = 0.738v^{-0.756} \ (r^2 = 0.993), \tag{2}$$

$$\text{Incline: } t_c = 0.642v^{-0.667} \ (r^2 = 0.966). \tag{3}$$

In all three of these equations, the exponent is significantly different from −1.0 (*P*<0.01).

Swing phase (Fig. 2B) averaged 3 % shorter (*P*=0.001) at all speeds when a horse was loaded than when it was on the level, and on the incline it averaged 6 % longer (*P*<0.001) at the three slowest speeds (2.0, 2.5 and 3.0 m s^{-1}). The duration of the swing phase (t_{sw}, with units of s) was a curvilinear function of
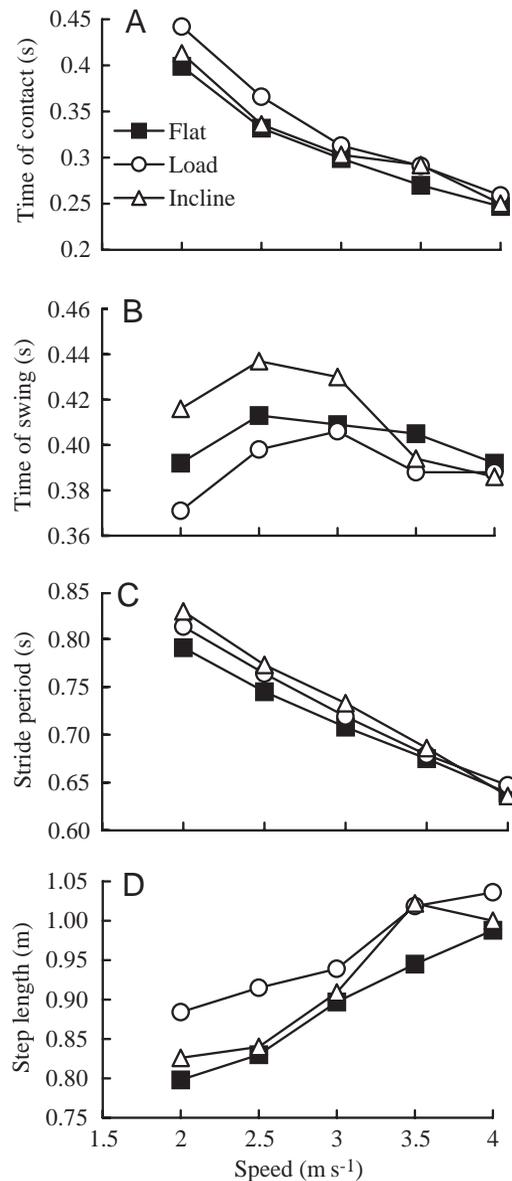

Fig. 2. (A) The time of contact was significantly longer when a horse was loaded than when it was trotting up an incline or unloaded on the level. Under all three conditions, time of contact decreased as a power function of speed. (B) The duration of the swing phase was significantly shorter at all speeds when a horse was loaded and significantly longer at low speeds when it was trotting up an incline. Under all three conditions, the swing phase was a nonlinear function of speed, with higher values at intermediate speeds than at high or low trotting speeds. (C) The stride period was significantly longer when a horse was loaded or trotting up an incline than when it was trotting on the level. (D) Step length was significantly longer when a horse was loaded than when it was trotting on the level or up an incline. Step length increased with speed under all three conditions.

trotting speed under all three conditions. The equations describing these relationships are:

$$\text{Level: } t_{sw} = -0.020v^2 + 0.117v + 0.239 \ (r^2 = 0.686), \quad (4)$$

$$\text{Load: } t_{sw} = -0.023v^2 + 0.141v + 0.184 \ (r^2 = 0.605), \quad (5)$$

$$\text{Incline: } t_{sw} = -0.029v^2 + 0.152v + 0.232 \ (r^2 = 0.714). \quad (6)$$

In each of these relationships, the quadratic term was significantly different from zero ($P<0.05$), indicating that the duration of the swing phase was greatest at intermediate trotting speeds.

The stride period (Fig. 2C) was significantly longer in loaded horses ($P=0.025$) and when trotting up an incline ($P=0.008$) than on the level. As a result, stride frequency on the incline was 2.2% slower than on the level and, when the horse was loaded, it averaged 1.6% slower than on the level.

Step length (Fig. 2D) calculated from the product of t_c and v, of necessity has the same statistical significance as t_c, but what is not obvious from the analysis of t_c is that step length increases with speed under all three experimental conditions.

Allometry of t_c and variation in step length in bipeds and quadrupeds

The data on the rate of force application ($1/t_c$) extracted from Kram and Taylor (1990) and Roberts et al. (1998) are reproduced in Fig. 3A. Least-squares linear regressions of the log-transformed values of t_c and speed are reported in Table 1, and the graphs appear in Fig. 3B. Only one of the slopes is not significantly different from zero (quail) and nine are significantly different from -1.0. The similarity between the slopes of these relationships suggested that t_c might be a similar function of speed in most of these species. A preliminary analysis indicated that leg length might account for the differences between species, so we performed a multiple regression of t_c on leg length (L, with units of m) and running speed (v) using log-transformed values and obtained the following relationship:

$$t_c = 0.80L^{0.84}/v^{0.87} \ (r^2 = 0.97). \quad (7)$$

Both the exponents in equation 7 are significantly different from zero ($P<0.001$), indicating that both variables contribute

Table 1. *Time of contact (s) as a power function of speed (m s^{-1}) in quadrupeds and bipeds*

Species	Body mass (kg)	N	B	A	r^2	Standard error of B	P: slope=0	P: slope=−1	Leg length (m)
Squirrel[1] *Spermophilus tridecemlineatus*	0.21	6	−0.865	0.103	0.998	0.020	<0.001	0.001	0.0984
Dog[1] *Canis familiaris*	25.8	6	−0.859	0.449	0.999	0.011	<0.001	<0.001	0.474
Pony[1] *Equus caballus*	141	6	−0.829	0.584	0.999	0.013	<0.001	<0.001	0.827
Horse[3] *Equus caballus*	450	5	−0.680	0.631	0.996	0.025	<0.001	<0.001	1.190
Kangaroo rat[1] *Dipodomys merriami*	0.032	3	−0.777	0.660	0.996	0.051	0.042	0.049	0.059
Spring hare[1] *Pedetes capensis*	3.0	3	−0.701	0.250	0.999	0.026	0.023	0.007	0.310
Human[2] *Homo sapiens*	78.88	6	−0.653	0.635	0.992	0.029	<0.001	<0.001	1.003
Bobwhite quail[2] *Colinus virginianus*	0.13	3	−0.593	0.164	0.955	0.129	0.136	0.087	0.114
Guinea fowl[2] *Numida meleagris*	1.3	4	−0.742	0.337	0.998	0.026	0.001	0.002	0.279
Turkey[2] *Meleagris gallopavo*	5.3	5	−0.756	0.447	0.998	0.018	<0.001	<0.001	0.483
Rhea[2] *Rhea americana*	19.9	7	−0.964	0.754	0.994	0.034	<0.001	0.324	0.809
Emu[2] *Dromaius novaehollandiae*	40.1	4	−0.881	0.858	0.988	0.070	0.006	0.184	1.003

The equations are presented in the form: $t_c = Av^B$, where t_c is time of contact and v is velocity.

Data sources for time of contact: [1]Kram and Taylor (1990); [2]Roberts et al. (1998); [3]Present study.

N, the number of speeds reported.

Standard error of B is the standard error of the slope (B).

P: slope=0 is based on a Student's t-test comparing the observed slope with a slope of zero; P: slope=−1 is based on a Student's t-test comparing the observed slope with a slope of −1.
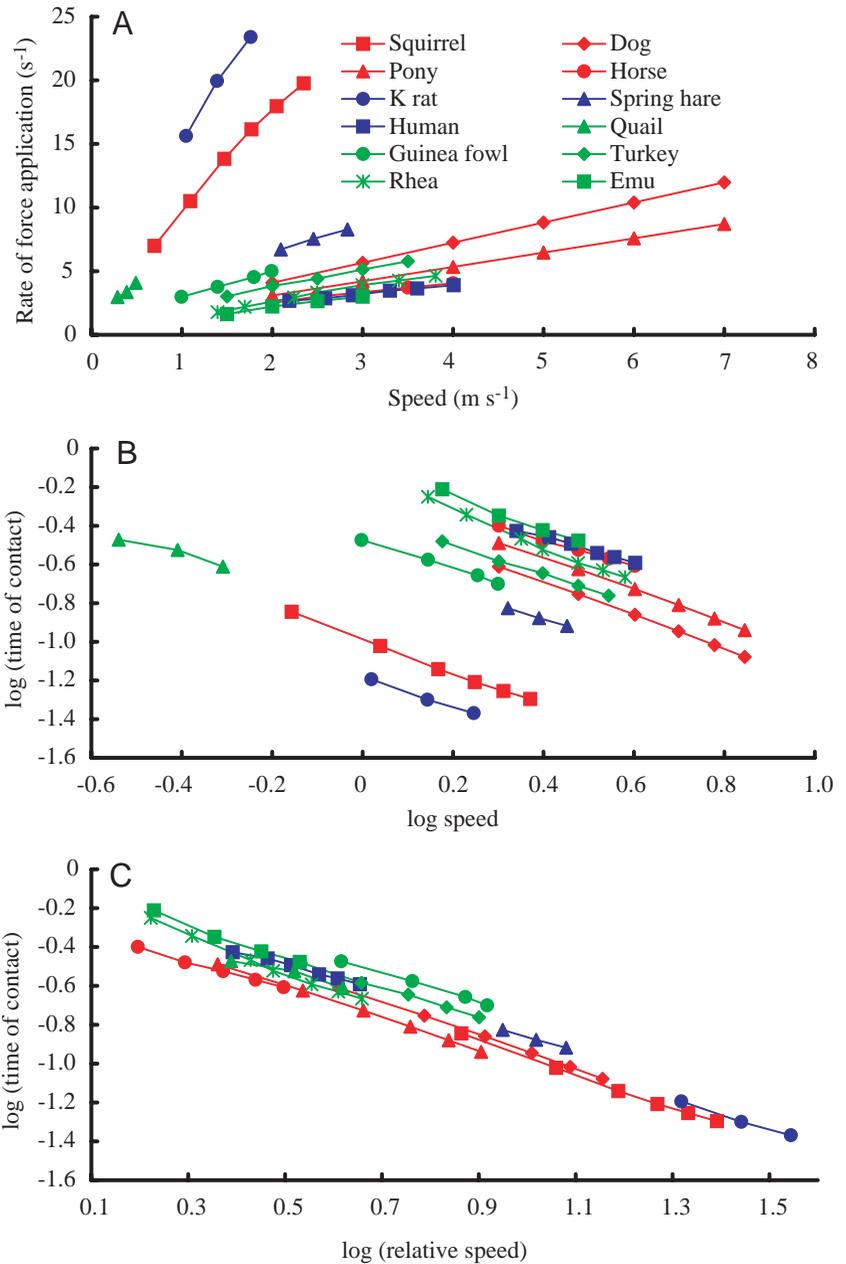
Sources for leg lengths are reported in the text.

Fig. 3. (A) The rate of force application (t_c^{-1}, where t_c is time of contact) increases as a linear function of speed within species. In addition, the slope varies in a regular manner with body mass, being steeper in smaller species. This relationship parallels the variation in mass-specific metabolic rate during running and suggests that the cost of generating force is the primary determinant of the cost of locomotion. Red symbols are for mammalian quadrupeds, blue symbols are for mammalian bipeds, and green symbols are for avian bipeds. The data for this figure were taken from Kram and Taylor (1990), Roberts et al. (1998) and the present study. (B) Time of contact is a power function of running speed with very similar slopes in 12 species of biped and quadruped. The data in this figure are those in A plotted on logarithmic axes as t_c (s) and speed (m s^{-1}). The slopes of the regressions are presented in Table 1. (C) Relative speed explains 97 % of the variability in time of contact. Relative speed (leg lengths s^{-1}) is calculated by dividing running speed by leg length. Leg length was predicted allometrically using the equations of Roberts et al. (1998). K rat, kangaroo rat.
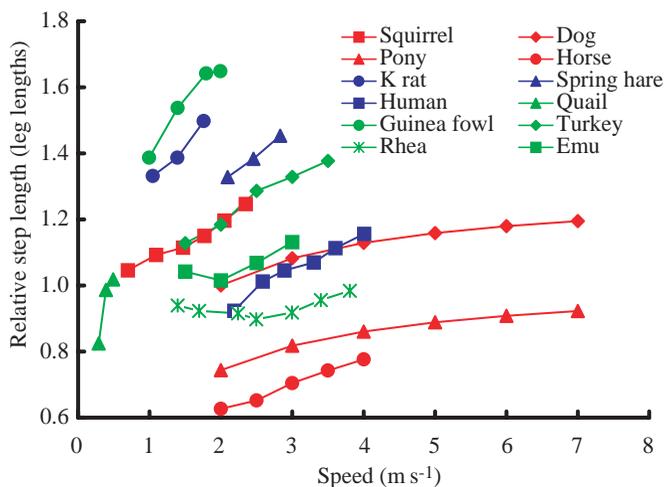
significantly to the prediction of t_c. A more intuitive representation of the relationship embodied in equation 7 is to plot t_c against 'relative running speed,' calculated by dividing running speed by leg length for each of the individual species. Relative running speed, therefore, has units of L s^{-1}. Fig. 3C is a graph of logt_c *versus* log(relative running speed). Both the exponents in equation 7 are also significantly different from 1.0 ($P<0.01$), the exponents implicitly assumed in calculating relative running speed ($v^{1.0}L^{-1.0}$). This means that Fig. 3C does

Fig. 4. Relative step length increases with speed in most species, and the average step length is shorter in larger species. Relative step length is calculated by dividing step length (l_c) by leg length (L). It represents the distance traveled by the center of mass during the stance phase when expressed in units of leg length. K rat, kangaroo rat.

not precisely represent the dependence of t_c on v and L: in Fig. 3C, there appears to be slightly more scatter in the data than is actually the case.

The fact that the exponents in equation 7 are significantly different from 1.0 suggests that step length (the product of running speed and time of contact) increases with speed and that the average step length used by different species varies with leg length. Step length was calculated from the values of t_c and v (m s^{-1}), and relative step length was obtained by dividing step length at all speeds by the leg length for each species. Relative step length (with units of leg lengths) increased with running speed for most species (Fig. 4).

Discussion

Time of contact is a function of speed and leg length

Time of contact (t_c, the duration of the stance phase of the stride cycle) is highly correlated with leg length (L) and running speed (v) in terrestrial bipeds and quadrupeds (Fig. 3C). This is particularly interesting because the inverse of time of contact (the rate of force application, Fig. 3A) has been shown to account for most of the speed-related and size-related differences in the metabolic cost of locomotion (Kram and Taylor, 1990; Roberts et al., 1998).

Quantifying the dependence of t_c on speed and leg length permits us to quantify two other important relationships. The spring-mass model (Farley et al., 1993) predicts that step length should increase with running speed, but no quantitative prediction is provided. Gatesy and Biewener (1991) report that small bipeds run with longer average relative step lengths than do large bipeds, but they did not quantify this relationship. The exponent for the relationship between t_c and speed (-0.87) is significantly different from -1.0; consequently, step length ($l_c = t_c v$) increases with speed (Fig. 4). This contradicts the simplifying assumption that step length is constant (Taylor, 1994), but is more consistent with the predictions of the spring-mass model (Farley et al., 1993) and with observations by the investigators who collected most of the data used in our analysis (Kram and Taylor, 1990; Roberts et al., 1998).

The exponent of the relationship between t_c and leg length (0.84) is significantly different from $+1.0$, leading to the conclusions that smaller animals run with average step lengths that are as much as 60 % longer than their leg length and that large animals run with average step lengths that are 25–30 % shorter than their leg length (Fig. 4). This size-dependence has been noted previously, but not quantified for bipeds (Gatesy and Biewener, 1991), and has not been reported for quadrupeds.

Taylor (1994) reasoned that it would be advantageous if step length were to remain constant because this would prevent a decline in the mechanical advantage of the anti-gravity muscles and minimize the increase in the metabolic cost of locomotion. However, the opposite appears to be the case: if step length were to remain constant, metabolic rate would increase more rapidly with speed than it does. For step length to remain constant, as speed doubled from 2 to 4 m s^{-1}, the time of contact would be halved and the rate of force application would double. Using our data on the level for comparison (Fig. 2A), at 2.0 m s^{-1} the time of contact was 0.40 s and at 4.0 m s^{-1} it was 0.25 s. Thus, the rate of force application increased from 2.5 to 4.0 s^{-1}, a 60 % increase. For step length to remain constant, it would have been necessary for the time of contact to decrease from 0.40 to 0.20 s, causing the rate of force application to increase from 2.5 to 5.0 s^{-1}, yielding a 100 % increase in the rate of force application. Keeping step length constant would have caused a 67 % larger increase in metabolic rate than is observed (100/60=1.67).

A comparison of the dependence of t_c on running speed and leg length indicated that there was a small difference between the bipeds and quadrupeds; however, the difference is small and more data are required before we can be certain that this difference is biologically significant. Some of the limitations of the current analysis are the following. First, the data set includes only three species of quadruped, the pony and horse being different breeds of the same species. However, the apparent difference between bipeds and quadrupeds depends primarily on the 11 data points obtained from these large, highly cursorial quadrupeds. Second, for statistical purposes, it is difficult to determine what value one should use for the sample size because different numbers of speeds (3–7) were used for each species. For all these reasons, it seems prudent to obtain more data before asserting that there is a biologically significant difference between bipeds and quadrupeds in the relationship between time of contact, speed and leg length.

The effect of load on time of contact in a horse is consistent with the hypothesis (Kram and Taylor, 1990) that time of contact determines the metabolic cost of locomotion. When carrying a load, a horse increases its time of contact (Fig. 2A). Because carrying a load increases the force that the locomotory muscles must generate in direct proportion to the load carried (Farley and Taylor, 1991), increasing the time of contact would be predicted to decrease the rate of force application and to minimize the metabolic cost of carrying the load.

The increased stride period (Fig. 2C) and time of contact (Fig. 2A) resulting from carrying a load in the present study differ from previous reports for animals (Taylor et al., 1980) and from some reports for humans (Cooke et al., 1991) but agree, in part, with another study in horses (Sloet Van Oldruitenborgh-Oosterbaan et al., 1995). Taylor et al. (1980) studied the effect of a load of 22 % of body mass on one 114 kg horse trotting at 2.7 m s^{-1} and 3.1 m s^{-1}. They reported that neither stride period nor time of contact was changed. There are several possible explanations for this difference: the small sample size used by Taylor et al. (1980) ($N=1$), counting stride frequency by hand or the accuracy of the method they used to determine time of contact (visually detecting hoof contact on 200 Hz cine film). One other observation that may help explain the difference from our results is that, in our animals, the difference in time of contact between the level and loaded conditions is smaller at a speed of 3.0 m s^{-1} than it is at any other trotting speed, averaging only 0.014 s. This would

represent less than three frames in the cine records of Taylor et al. (1980). It is also possible that the difference can be attributed to differences in the different amount of physical conditioning provided to the animals in the present study and in that of Taylor et al. (1980). Dutch Warmblood horses (median mass 632 kg), trotting at 4.0 m s^{-1} and carrying a 90 kg load (=14 % of body mass) increase t_c by an average of 0.017 s, but do not increase stride period (Sloet Van Oldruitenborgh-Oosterbaan et al., 1995). Load-carrying in humans has been reported to increase (Cooke et al., 1991; Thorstensson, 1986) or not to affect (Davies, 1980) stride period.

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