

SPEED, STRIDE FREQUENCY AND ENERGY COST PER STRIDE: HOW DO THEY CHANGE WITH BODY SIZE AND GAIT?

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Summary

In this study we investigate how speed and stride frequency change with body size. We use this information to define 'equivalent speeds' for animals of different size and to explore the factors underlying the six-fold difference in mass-specific energy cost of locomotion between mouse- and horse-sized animals at these speeds. Speeds and stride frequencies within a trot and a gallop were measured on a treadmill in 16 species of wild and domestic quadrupeds, ranging in body size from 30 g mice to 200 kg horses. We found that the minimum, preferred and maximum sustained speeds within a trot and a gallop all change in the same rather dramatic manner with body size, differing by nine-fold between mice and horses (i.e. all three speeds scale with about the 0.2 power of body mass). Although the absolute speeds differ greatly, the maximum sustainable speed was about 2.6-fold greater than the minimum within a trot, and 2.1-fold greater within a gallop. The frequencies used to sustain the equivalent speeds (with the exception of the minimum trotting speed) scale with about the same factor, the -0.15 power of body mass. Combining this speed and frequency data with previously published data on the energetic cost of locomotion, we find that the mass-specific energetic cost of locomotion is almost directly proportional to the stride frequency used to sustain a constant speed at all the equivalent speeds within a trot and a gallop, except for the minimum trotting speed (where it changes by a factor of two over the size range of animals studied). Thus the energy cost per kilogram per stride at five of the six equivalent speeds is about the same for all animals, independent of body size, but increases with speed: $5.0 \text{ J kg}^{-1} \text{ stride}^{-1}$ at the preferred trotting speed; $5.3 \text{ J kg}^{-1} \text{ stride}^{-1}$ at the trot–gallop transition speed; $7.5 \text{ J kg}^{-1} \text{ stride}^{-1}$ at the preferred galloping speed; and $9.4 \text{ J kg}^{-1} \text{ stride}^{-1}$ at the maximum sustained galloping speed. The cost of locomotion is determined primarily by the cost of activating muscles and of generating a unit of force for a unit of time. Our data show that both these costs increase directly with the stride frequency used at equivalent speeds by different-sized animals. The increase in cost per stride with increasing speed may be related to differences in mechanical advantage of the limb muscles (necessitating higher muscle forces for the same ground reaction force) as stride length increases both in the trot and in the gallop.

Key words: locomotion, mechanics, energetics.

Introduction

During locomotion, each gram of muscle consumes energy at a much higher rate in a small animal than in a large animal (Taylor *et al.* 1970), yet this higher metabolic rate has not been found to be associated with higher rates of mechanical work performance (Heglund *et al.* 1982). For example, on a per gram basis, a 30 g mouse consumes energy at six times the rate of a 300 kg horse at the 'equivalent' speed where they shift gaits from a trot to a gallop, although the per gram rate of mechanical work performed to sustain this speed is essentially the same for both animals. If the rate at which muscles perform mechanical work does not determine the energy cost of locomotion, then what does?

An important clue is provided by the close association between stride frequency and energy cost. The small animal's higher costs of locomotion are associated with higher stride frequencies (Heglund *et al.* 1974). In fact, stride frequency has been found to be directly associated with the energetic cost of locomotion in a simple one-to-one relationship at the speed where quadrupeds change from a trot to a gallop (Heglund *et al.* 1982). At this speed the 30 g mouse takes six times as many strides per second as the 300 kg horse, yet the cost per gram per stride is identical.

We propose that the costs involved both in activating muscle and in generating a unit of force for a unit of time by each gram of muscle are directly proportional to stride frequency at all equivalent speeds, and that this explains the relationship between the cost of locomotion and body size. The purpose of this paper is to test these ideas. First, we determine how the range of speed within two quadrupedal gaits (trot and gallop) changes with body size. We have limited our study to these two gaits because we have not been successful in making steady-state measurements over a range of walking speeds in small quadrupeds. Second, we determine how stride frequency changes with speed over the entire speed range for each gait. Third, we determine how stride frequency changes with body size at equivalent points within each gait: the slowest speed, the speed at the mid-point in the gait (the speed which animals prefer to use in nature) (Pennycuik, 1975; Perry *et al.* 1988), and the fastest sustainable speed. These relationships, which are presented in the Results section of this paper, are used together with published data on energy consumption in the same species to address two questions. (1) Is the energy cost of locomotion per gram directly proportional to stride frequency at equivalent points in the speed range of each gait in animals of different size? (2) How does cost per gram per stride change with speed within each gait? Finally, we will relate our findings in whole animals to what is known about the costs of activating and generating force by muscles.

Materials and methods

Animals

We obtained nine species of wild and domestic artiodactyls, and one species of perissodactyl by capture or purchase in Kenya. The artiodactyls, in order of increasing body size, were: two suni (*Nesotragus moschatus*, 3.5 kg); two dik-diks

(*Madoqua kirkii*, 4.35 kg); one Grant's gazelle (*Gazella granti*, 11.2 kg); two African domestic goats (*Capra hircus*, 20 kg); two fat-tailed sheep (*Ovis aries*, 23 kg); two wildebeest (*Connochaetes taurinus*, 98 kg); two waterbucks (*Kobus defassa*, 114 kg); two zebu cattle (*Bos indicus*, 160 kg); and two elands (*Taurotragus oryx*, 213 kg). The perissodactyl was a domestic donkey (*Equus asinus*, 170 kg). All these animals were housed at facilities provided by the East African Veterinary Research Organization, Muguga, Kenya.

We obtained six species of wild and domestic rodents, carnivores and perissodactyls by capture or purchase in the United States. In order of increasing size these were: three laboratory mice (*Mus musculus*, 0.029 kg); two chipmunks (*Tamias striatus*, 0.061 and 0.107 kg); three 13-lined ground squirrels (*Spermophilus tridecemlineatus*, 0.193 kg); three white rats (*Rattus norvegicus*, 0.362 kg); five domestic dogs (*Canis familiaris*, 0.96, 3.89, 9.21, 19.9 and 25 kg); three ponies and one horse (*Equus caballus*, 110, 140, 170 and 680 kg). These animals were housed in facilities with adequate space for voluntary exercise at the Concord Field Station, Harvard University.

Methods

The animals were trained to run on a treadmill. After at least several weeks of training, the stride frequency was measured while the animals ran at a constant tread speed on the level. Stride frequency was determined in each gait by timing the interval for 25 cycles of one foot, e.g. the front right foot; although sometimes fewer than 25 cycles were counted (usually in the smallest animals). Large animals were timed with a stopwatch; small animals were timed using a high-speed camera at 100–200 frames s^{-1} , either an Eclair GV-16 with a high-speed clock in the film view or, in a few cases, a Photosonics 1PL with a clock mark automatically registered on the side of the film.

The stride frequency vs speed data for each gait were fitted to a straight line using the least-squares fit method. The trot–gallop transition speed was determined from the intersection of the two regression lines. The stride frequency vs body size relationships were determined by using a least-squares fit regression on log-transformed data. Mean values are given \pm s.e., except where otherwise stated.

Results

Walk

The data we obtained for walking are not sufficient to describe a function relating frequency to speed over a wide range of body size. It proved very difficult to obtain data from small animals walking at a constant average speed on the treadmill. The mice, chipmunks and white rats normally maintained slow average speeds by running to the front of the treadmill, stopping, and riding to the back. The animals sustained these oscillations for long periods without utilizing a steady-speed walk. We have included measurements of walking frequency as a function of

speed in Fig. 1 for animals that sustained a constant speed walk, even though we have not been able to develop allometric relationships for this gait.

Trot

Small animals began to trot at much slower speeds than did large animals. The minimum trotting speed increased by about nine-fold over the size range from a 30 g mouse to a 170 kg horse (from 0.19 to 1.8 m s⁻¹, Table 1). The speed at which the animals changed from a trot to a gallop also increased with body size with approximately the same size-dependency as the minimum trotting speed: minimum trotting speed increased with the 0.25 power of body mass and trot-gallop transition speed with the 0.22 power. The allometric equations and confidence intervals relating minimum, preferred and trot-gallop transition speeds to body mass are given in Table 2. The speed range within a trot was on average 2.58 ± 0.25 (S.E.) times the minimum trotting speed. The variability in this 2.58-fold scope appeared to be independent of body size.

Table 1. *Stride frequency during trotting, plotted in Fig. 1, is used to calculate least-squares fit linear regression equations relating stride frequency to running speed*

Animal	Body mass (kg)	Intercept (strides s ⁻¹)	Slope (strides m ⁻¹)	N	Speed range	
					Minimum (m s ⁻¹)	Maximum (m s ⁻¹)
White mouse*	0.029	1.80	7.33	1	0.19	0.54
13-lined ground squirrel	0.193	2.88	2.76	3	0.67	1.45
White rat*	0.362	0.58	5.74	3	0.11	0.61
Dog*	0.96	1.02	2.58	1	0.84	1.14
Suni	3.5	0.985	1.09	2	1.15	1.74
Dog*	3.89	1.64	0.63	1	1.39	2.68
Dik-dik	4.35	0.94	1.02	2	0.99	2.01
Dog*	9.21	1.51	0.49	1	1.15	3.53
Grant's gazelle	11.2	1.25	0.325	1	1.53	3.12
African domestic goat	20	0.869	0.70	1	1.53	2.44
Fat-tailed sheep	23	1.236	0.497	2	1.41	2.41
Dog*	25	1.06	0.34	1	1.25	4.03
Wildebeest	98	1.12	0.274	1	1.89	3.06
Pony	110	1.20	0.25	1	1.64	4.28
Waterbuck	114	1.34	0.104	3	1.92	4.39
Pony	140	1.22	0.21	1	1.69	4.64
Zebu cattle	160	1.13	0.213	2	2.08	3.66
Pony	170	1.09	0.25	1	1.81	4.78
Donkey	170	1.12	0.22	1	1.80	4.75
Eland	213	1.17	0.136	1	1.75	5.67
Horse*	680	0.623	0.25	31	1.42	5.46

The equations are presented in the form: stride frequency = intercept + (slope × speed), where stride frequency is in strides s⁻¹ and speed is in m s⁻¹; N is the number of animals analysed.

Asterisks indicate data previously published by Heglund *et al.* (1974).

Table 2. Allometric equations relating five 'equivalent' speeds within a trot and gallop to body size

Equivalent speed	Coefficient a	Exponent b	r^2
Minimum trotting speed	0.593 (0.444, 0.791)	0.249 (0.169, 0.329)	0.70
Preferred trotting speed	1.09 (0.913, 1.31)	0.222 (0.172, 0.272)	0.83
Trot-gallop transition speed	1.54 (1.28, 1.86)	0.216 (0.163, 0.268)	0.81
Preferred galloping speed	2.78 (2.37, 3.26)	0.176 (0.131, 0.221)	0.76
Maximum sustained galloping speed	3.71 (3.16, 4.34)	0.176 (0.131, 0.221)	0.76

The equations are presented in the form: speed = $a(M_b)^b$, where speed is in m s^{-1} and M_b is in kg.

The coefficient of determination (r^2) between the logarithm of speed and the logarithm of M_b is given for each equation.

The 95 % confidence limits for each coefficient a and each exponent b are given in parentheses below the mean value.

Stride frequency increased nearly linearly with increasing speed during a trot in all the quadrupeds (Fig. 1); however, small animals used higher frequencies than larger animals. All the animals increased stride frequency by an average of 1.55 ± 0.12 times as they increased their speed from their lowest trotting speeds to the trot-gallop transition speed (Table 1). There was remarkably little variability in this 1.55-fold scope, despite the large variability in speed range within a trot. The slope of the function relating stride frequency to speed decreased dramatically with body size, e.g. by about 30-fold between a mouse and a horse (Table 1). It is interesting that the stride frequency at the extrapolated zero velocity did not show this marked size-dependency, and was similar for all the animals (mean 1.23 ± 0.11 Hz).

The speed at the middle of the trotting range is the speed that animals in nature prefer to use when they trot (Hoyt & Taylor, 1981; Perry *et al.* 1988). Therefore, it provides an equivalent trotting speed for comparing animals of different size. The stride frequency measured as the preferred trotting speed decreased in a regular manner with increasing body size. The preferred trotting speed and the stride frequency at this speed are plotted as a function of body mass on logarithmic coordinates in Fig. 2A and can be expressed by the allometric equations:

$$\text{preferred trotting speed} = 1.09M_b^{0.222}, \quad (1)$$

$$\text{frequency at preferred trotting speed} = 3.35M_b^{-0.130}, \quad (2)$$

where speed has the units of m s^{-1} , frequency is in strides s^{-1} , and M_b is in kg. The 95 % confidence limits for these allometric equations are given in Tables 2 and 3.

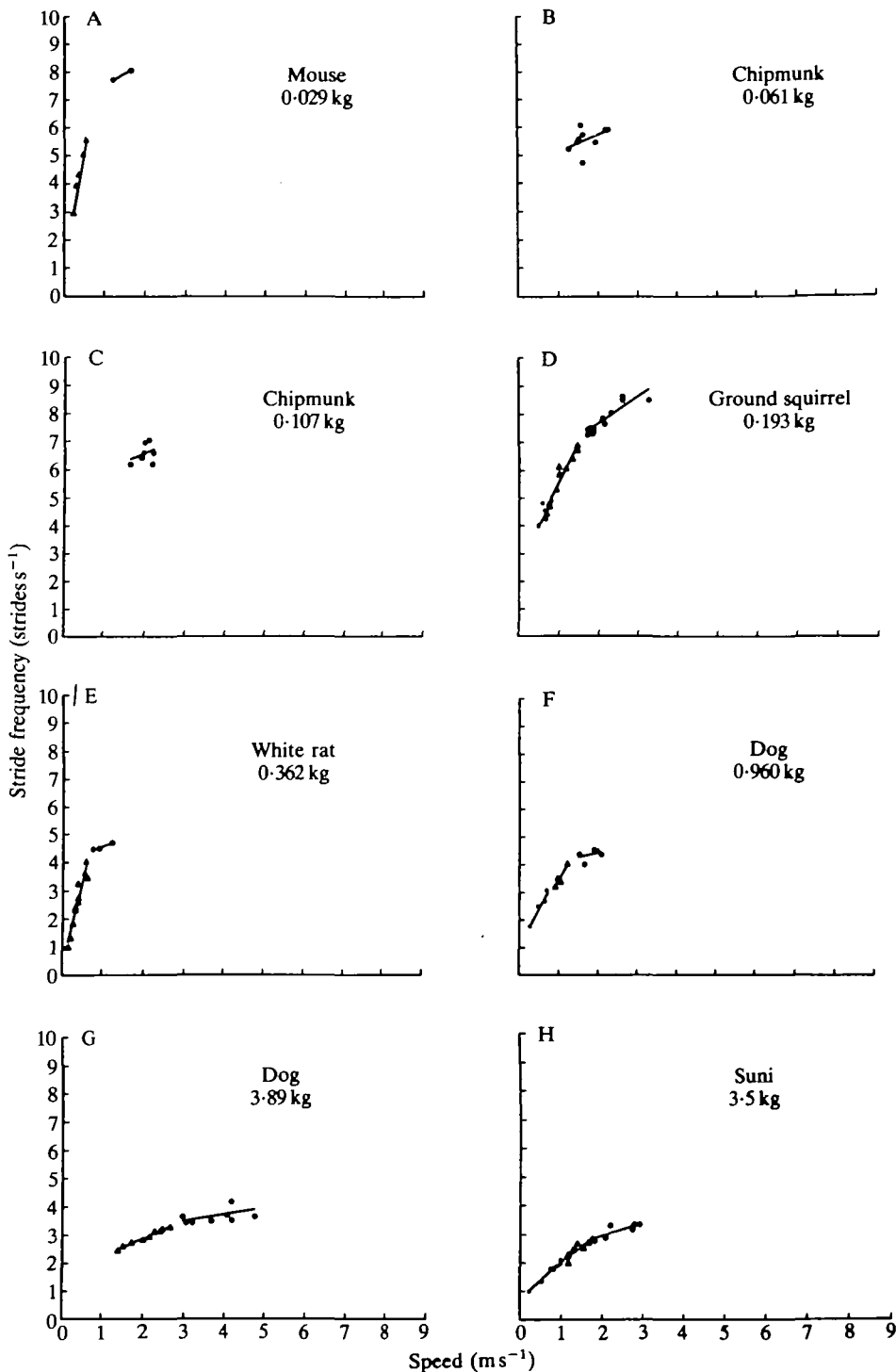


Fig. 1A-H

Fig. 1. For legend see p. 309.

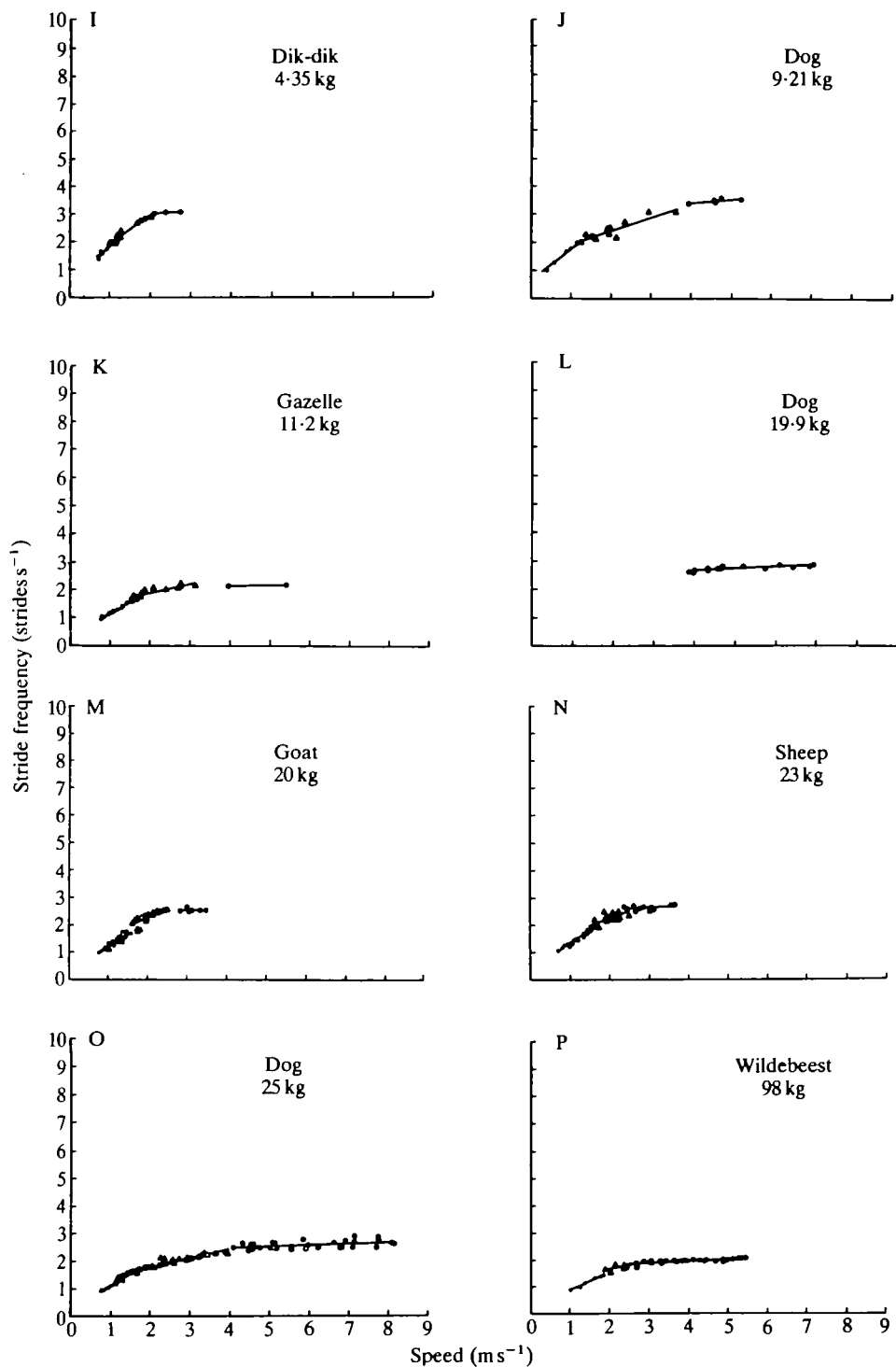


Fig. 11-P

Fig. 1. For legend see p. 309.

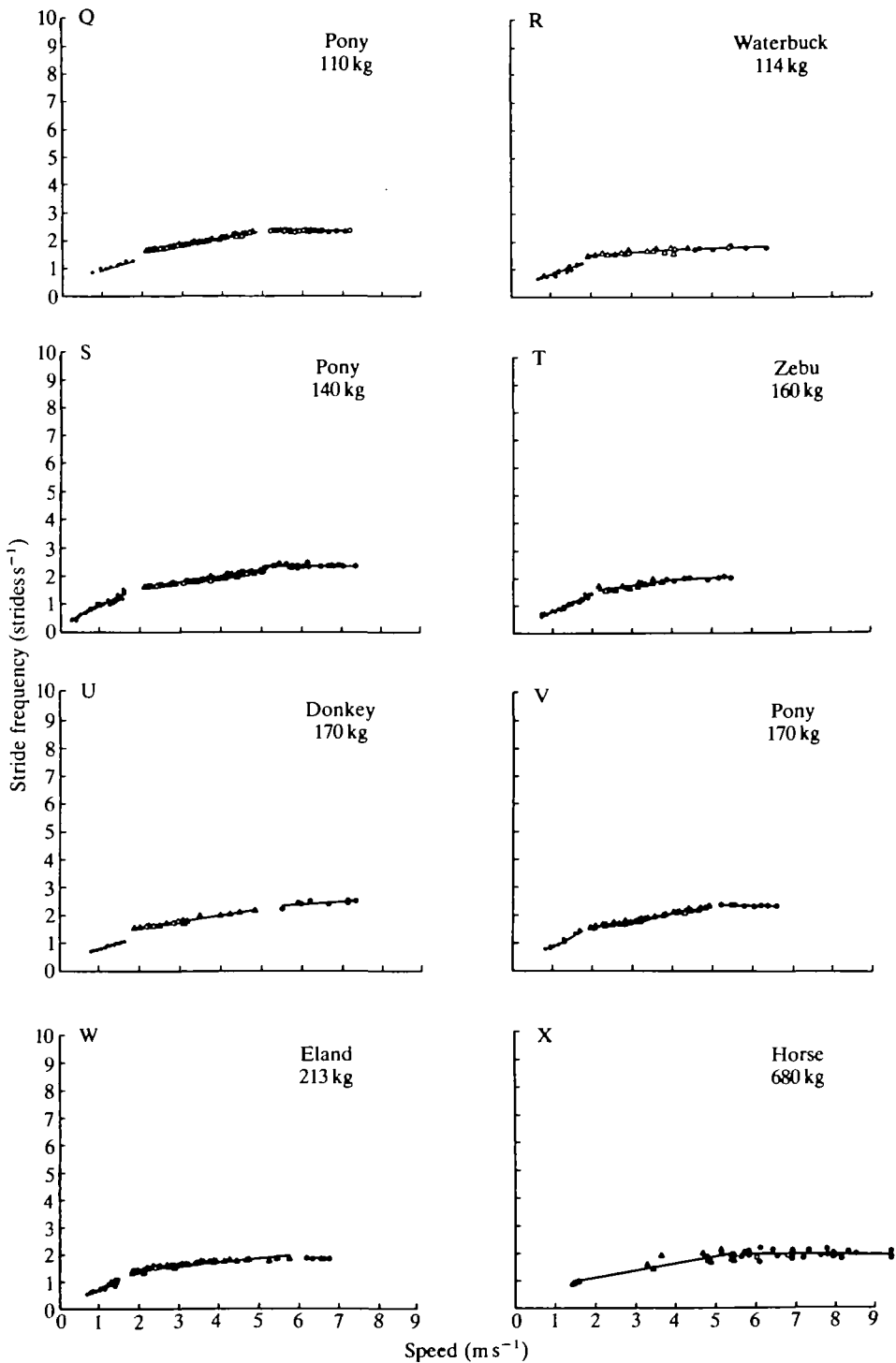


Fig. 1Q-X

Trot-gallop transition

Under steady-state conditions, the maximum trotting speed and minimum galloping speed were the same, i.e. the trot-gallop transition speed. We were not always able to obtain measurements precisely at the transition speed, but when we did the animals sustained a constant speed for long periods while oscillating between the two gaits. It is interesting that the stride frequency was the same whether animals trotted or galloped at this speed, i.e. the two functions relating stride frequency to speed during a trot and during a gallop intercept at the transition speed. Thus the transition speed can be defined accurately by extrapolating the functions to the speed where they intersect, without measurements at the exact speed.

Animals normally show a hysteresis with respect to gait when tread speed is changed on a treadmill. As speed increases, the animal will maintain a trot to speeds above the trot-gallop transition speed for short periods before switching to a gallop. Similarly, as speed decreases the animal will maintain a gallop to speeds below the trot-gallop transition speed for short periods before switching to a trot. In these studies, care was taken to avoid this hysteresis by waiting until animals had achieved steady-state conditions at a given tread speed.

Speed and stride frequency at the trot-gallop transition are plotted as a function of body mass in Fig. 2B. Although animals would probably not use this speed if given a choice, it is very useful for comparisons of different animals because it can be measured easily and precisely in the laboratory, whereas top speed and speed at the middle of the galloping range cannot. Additionally, it has been used in previous studies relating stride frequency and body size (Heglund *et al.* 1974) and is useful for comparing the data presented here with previously published data relating stride frequency to body size. The allometric equations relating the speed and stride frequency at the trot-gallop transition to body mass are:

$$\text{trot-gallop transition speed} = 1.54M_b^{0.216}, \quad (3)$$

$$\text{frequency at trot-gallop transition} = 4.19M_b^{-0.150}, \quad (4)$$

where speed has the units m s^{-1} , frequency is in strides s^{-1} and M_b is in kg. The 95 % confidence limits for these allometric equations are given in Tables 2 and 3.

Gallop

Small animals switch from a trot to a gallop at much lower speeds than do large animals (Fig. 1). This speed increases with the 0.22 power of body mass (equation 3). For example, a 30 g mouse began to gallop at a speed of 0.8 m s^{-1} ,

Fig. 1. Stride frequency plotted as a function of speed for 16 species of quadrupedal mammals. Data obtained when animals moved at a steady speed during a walk are indicated by solid circles, during a trot by open triangles, and during a gallop by open circles. The equations representing stride frequency as a function of speed for a trot and a gallop (obtained by linear regression analysis of the data contained in each panel of the figure) are given in Table 1 (trot) and Table 4 (gallop). The minimum and maximum sustained speeds within each gait are also given in these Tables.

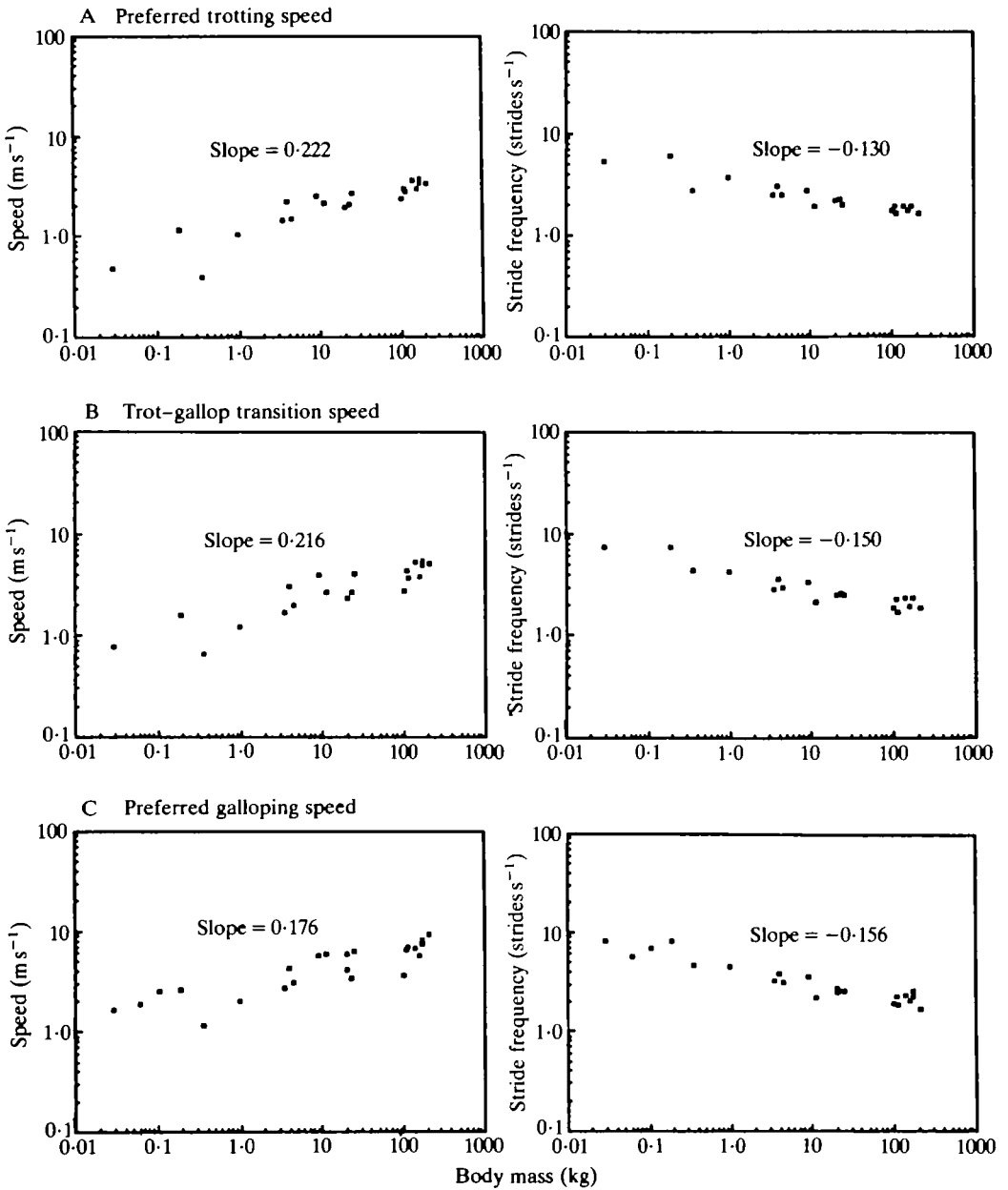


Fig. 2. (A) The preferred trotting speed and the stride frequency used at this speed plotted as a function of body mass on logarithmic coordinates. (B) The trot-gallop transition speed and the stride frequency used at this speed. (C) The preferred galloping speed and the frequency used at this speed. The allometric equations for each of these speeds as a function of body mass were determined by linear regression analysis of the log-transformed data, and are given in Table 2; the equations for the stride frequencies used at each of these speeds as a function of body mass are given in Table 3.

Table 3. Allometric equations relating the stride frequency used by quadrupeds at five 'equivalent' speeds to body size

Stride frequency at the following equivalent speeds	Coefficient <i>a</i>	Exponent <i>b</i>	<i>r</i> ²
	Mean (95 % confidence limits)	Mean (95 % confidence limits)	
Minimum trotting speed	2.42 (2.05, 2.85)	-0.091 (-0.045, -0.136)	0.50
Preferred trotting speed	3.35 (2.90, 3.50)	-0.130 (-0.099, -0.149)	0.84
Trot-gallop transition speed	4.19 (3.78, 4.65)	-0.150 (-0.120, -0.179)	0.87
Trot-gallop transition speed*	4.48	-0.147	0.99
Preferred galloping speed	4.44 (4.08, 4.84)	-0.156 (-0.131, -0.180)	0.90
Maximum sustained galloping speed	4.70 (4.28, 5.16)	-0.162 (-0.136, -0.189)	0.88

* Equation published by Heglund *et al.* (1974).

The equations are presented in the form: stride frequency = $a(M_b)^b$, where stride frequency is in strides s⁻¹ and M_b is in kg.

The coefficient of determination (r^2) between the logarithm of the stride frequency and the logarithm of M_b is given for each equation.

The 95 % confidence limits for each coefficient *a* and each exponent *b* are given in parentheses below the mean value.

whereas a 170 kg pony began to gallop at a speed of 5 m s⁻¹. It was not possible to obtain measurements over the entire speed range for the gallop in our treadmill studies because the measurements were made during steady-state locomotion where the energy is being supplied primarily by aerobic metabolism. Animals that are highly adapted for aerobic endurance, such as dogs and horses, provided us with much greater speed ranges than less aerobic animals such as goats and cattle. All animals were capable of short bursts at higher galloping speeds by relying to a greater extent on anaerobic metabolism. It seems likely that anaerobic capabilities, like aerobic capabilities, vary among species. Top galloping speed is the fastest speed the quadrupedal animals can achieve and, as yet, we lack any reliable criteria for being certain that we have achieved this experimentally, either in the laboratory or in nature. The highest galloping speeds that we measured were on average 2.11 ± 0.072 times the lowest galloping speeds where the animals switched from a trot to a gallop.

Stride frequency within a gallop increased very little with increasing speed, typically about 10 % for a doubling of speed (Fig. 1). The larger animals used lower frequencies; for example, a mouse gallops using a stride frequency of about 7.9 Hz, whereas a horse gallops with a frequency of about 2.0 Hz. The slopes and intercept values for the least-squares linear regressions relating stride frequency to speed for all the data presented in Fig. 2 are given in Table 4.

Table 4. *Stride frequency during galloping, plotted in Fig. 1, is used to calculate least-squares fit linear regression equations relating stride frequency to running speed*

Animal	Body mass (kg)	Intercept (strides s ⁻¹)	Slope (strides m ⁻¹)	N	Speed range	
					Minimum (ms ⁻¹)	Maximum (ms ⁻¹)
White mouse*	0.029	6.86	0.780	3	1.10	1.54
Chipmunk	0.061	4.58	0.590	1	1.27	2.25
Chipmunk	0.107	5.32	0.606	1	1.68	2.25
13-lined ground squirrel	0.193	5.77	0.949	3	1.71	3.28
White rat*	0.362	4.08	0.532	3	0.77	1.23
Dog*	0.96	3.81	0.327	1	1.35	1.91
Suni	3.5	2.07	0.454	2	1.79	2.92
Dog*	3.89	2.84	0.235	1	2.84	4.62
Dik-dik	4.35	2.74	0.131	2	2.03	2.72
Dog*	9.21	2.92	0.129	1	3.75	5.06
Grant's gazelle	11.2	2.06	0.023	1	3.94	5.39
Dog	19.9	2.42	0.069	1	3.86	6.94
African domestic goat	20	2.49	0.005	1	2.75	3.39
Fat-tailed sheep	23	2.34	0.083	2	2.28	3.56
Dog*	25	2.27	0.050	1	4.17	8.25
Wildebeest	98	1.68	0.073	1	2.44	5.44
Pony	110	2.31	-0.005	1	4.33	6.31
Waterbuck	114	1.52	0.055	3	4.56	6.33
Pony	140	2.30	0.010	1	4.53	6.75
Zebu cattle	160	1.71	0.064	2	3.78	5.39
Pony	170	2.48	-0.026	1	4.97	6.33
Donkey	170	1.80	0.097	1	5.42	7.22
Eland	213	2.04	-0.035	1	6.11	6.67
Horse*	680	1.81	0.019	31	5.63	11.1

The equations are presented in the form: stride frequency = intercept + (slope × speed), where stride frequency is in strides s⁻¹ and speed is in ms⁻¹; N is the number of animals analysed.

Asterisks indicate data previously published by Heglund *et al.* (1974).

As in the trot, animals have a preferred speed in a gallop. This preferred speed is in the middle of the galloping speed range. We have selected the galloping speed in the middle of the observed galloping speed range as the best approximation we have of the preferred galloping speeds animals might use in nature. It is not as reliable as the mid-trot speed since we have not measured the entire galloping speed range. However, even if errors in speed introduced by this approximation are large, little error is introduced in the stride frequency, since the galloping frequency is nearly independent of speed.

Preferred galloping speed and stride frequency at this speed both changed in a regular manner with body size and are plotted as a function of body mass on

logarithmic coordinates in Fig. 2C. The allometric equations relating preferred galloping speed and frequency to body mass are:

$$\text{preferred galloping speed} = 2.78M_b^{0.176}, \quad (5)$$

$$\text{frequency at preferred galloping speed} = 4.44M_b^{-0.156}, \quad (6)$$

where preferred galloping speed has the units m s^{-1} , frequency is in strides s^{-1} and M_b is in kg. The 95 % confidence limits for these allometric equations are given in Tables 2 and 3.

Discussion

Our results demonstrate that the minimum, preferred and maximum speeds within a trot and a gallop, together with the stride frequencies used at these speeds, change in a regular and predictable manner with body size. Small animals are slower, have a smaller range of speeds, and use higher frequencies than do larger animals. However, we find that the relative increases in both frequency and speed are similar over the entire size range of animals. For example, a mouse and a horse both increase their speed by a factor of about 2.6 within each gait. Both animals increase stride frequency by about 1.6-fold to achieve this increase in speed in a trot, and both animals increase stride frequency by only about 10 % as they increase their speed by 2.1-fold in a gallop.

The mechanics of each of these gaits are similar among mammals. Muscles and tendons serve as springs, alternately storing and releasing elastic strain energy as the animals 'bounce' along at a constant speed (Cavagna *et al.* 1977). The minimum and maximum speeds within each gait define the normal limits in the range of adjustment of the spring mechanism, and in this sense are 'mechanically equivalent' speeds in different animals. Furthermore, there is mounting evidence that stress (force/cross-sectional area) in the major components of the locomotory system (muscles, tendons and bones) reaches similar levels at these limits (Alexander, 1981; Biewener, 1982; Biewener & Taylor, 1986; Rubin & Lanyon, 1984; Perry *et al.* 1988).

In this study we selected five equivalent speeds for comparing animals of different size: (1) the minimum trotting speed; (2) the preferred trotting speed (in the middle of the trotting range); (3) the speed at which the animals normally change from a trot to a gallop; (4) the preferred galloping speed (in the middle of the galloping range); and (5) the maximum sustained galloping speed. Terrestrial animals exhibit a clear preference for the speeds and frequencies they use within each gait in nature. These preferred speeds were first observed by Pennycuik (1975) in wildebeest, gazelles and zebras as they migrated across the African plains, and have also been observed in a variety of wild and domestic species in the laboratory (Hoyt & Taylor, 1981; Perry *et al.* 1988). Preferred speeds fall in the middle of the speed range within each gait, and the preferred frequencies and speeds obtained from animals in nature agree well with those we measure on treadmills (Pennycuik, 1975; Hoyt & Taylor, 1981). We have found that all these

preferred speeds increase with body size with approximately the same scaling factor, the 0.21 power of body mass (Table 2). The stride frequency used at each of these speeds also changes with approximately the same scaling factor, the -0.14 power of body mass (Table 3). The equations relating mid-gallop and trot-gallop stride frequency to body mass are essentially the same. This was to be expected, since galloping frequency is nearly independent of speed. Also these equations, based on 16 species of quadrupeds, do not differ from an earlier equation relating stride frequency at the trot-gallop transition speed to body mass, which was based on data from only four species of quadrupeds (Heglund *et al.* 1974).

We can now consider the energy cost per gram per stride at each of these mechanically equivalent speeds. Using the relationships developed in this paper between speed, stride frequency and body mass, and the relationships described in an earlier paper between energy consumption, speed and body mass for each of these species (Taylor *et al.* 1982), we have calculated the energy cost per kilogram per stride (using an energy equivalent of $1 \text{ ml O}_2 = 20.1 \text{ J}$) for each of the animals of this study at each of the five equivalent speeds (Fig. 3; Table 5). We confirm our earlier finding that cost per kilogram per stride at the trot-gallop transition speed is nearly constant over the entire size range of animals from mice to horses (Heglund *et al.* 1982). There is remarkably little variation in this cost ($5.34 \pm 0.25 \text{ J kg}^{-1} \text{ stride}^{-1}$) considering the nine-fold differences in speed and the four- to five-fold differences in stride frequency used by the animals in this study at this gait transition. Experimentally, this is the best-defined speed and frequency, and shows the least variation.

Table 5. *Allometric equations relating energy cost per kilogram per stride to body size at five equivalent speeds*

Energy cost per gram per stride at the following equivalent speeds	Coefficient <i>a</i>	Exponent <i>b</i>	<i>r</i> ²
	Mean (95 % confidence limits)	Mean (95 % confidence limits)	
Minimum trotting speed	5.32 (4.56, 6.20)	-0.108 (-0.065 , -0.150)	0.61
Preferred trotting speed	5.35 (4.68, 6.12)	-0.046 (-0.008 , -0.083)	0.27
Trot-gallop transition speed	5.39 (4.70, 6.19)	-0.011 (-0.049 , 0.027)	0.02
Preferred galloping speed	7.21 (6.20, 8.39)	0.04 (-0.039 , 0.047)	0.00
Maximum sustained galloping speed	8.66 (7.36, 10.18)	0.018 (-0.029 , 0.064)	0.03

The equations are presented in the form: energy cost $\text{kg}^{-1} \text{ stride}^{-1} = a(M_b)^b$, where energy cost has the units $\text{J kg}^{-1} \text{ stride}^{-1}$ and M_b is in kg.

The coefficient of determination (r^2) between the logarithm of the stride frequency and the logarithm of energy cost $\text{kg}^{-1} \text{ stride}^{-1}$ and the logarithm of M_b are given for each equation.

The 95 % confidence limits for each coefficient *a* and each exponent *b* are given in parentheses below the mean value.

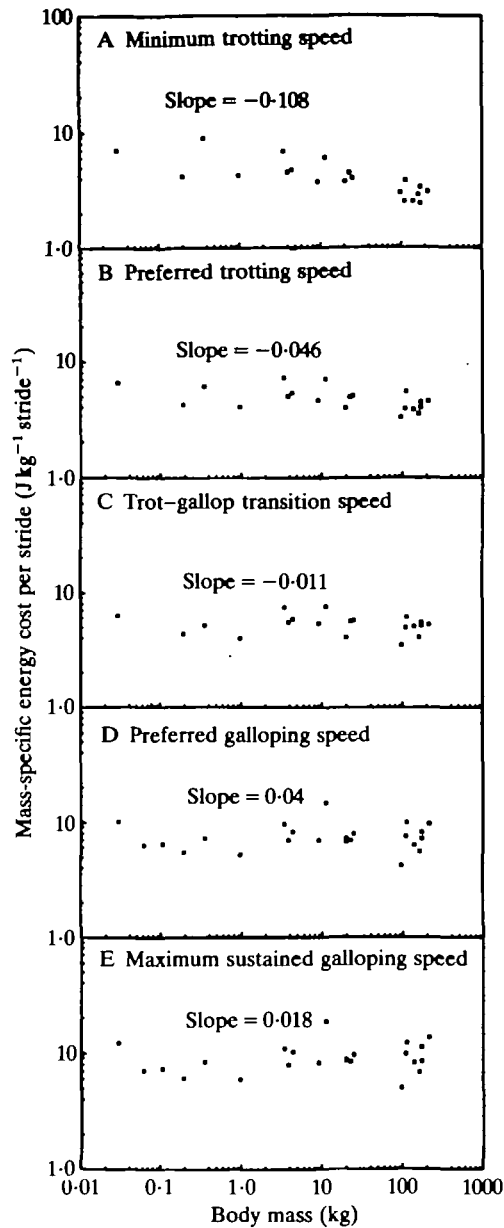


Fig. 3. The mass-specific energy cost per stride plotted as a function of body mass on logarithmic coordinates for five equivalent speeds: the minimum sustained trotting speed (A); the preferred trotting speed (B); the trot-gallop transition speed (this transition speed is both the maximum sustained trotting speed and the minimum sustained galloping speed) (C); the preferred galloping speed (D); and the maximum sustained galloping speed (E). The allometric equations for the mass-specific energy cost per stride at each of these preferred speeds were determined by linear regression analysis of the log-transformed data, and are given in Table 5.

The cost per gram per stride at the minimum trotting speed shows a slight size-dependency, scaling with the -0.108 power of body mass. This amounts to a cost 2.5 times greater in a 30 g mouse than a 270 kg horse. This is not surprising because the mechanics of walking involves a pendulum mechanism which may have a different size-dependency from the spring mechanism utilized in a trot and a gallop. This size-dependency becomes insignificant at the preferred trotting speed, scaling with body mass to the -0.046 . The cost at the trot-gallop transition speed, preferred galloping speed and maximum galloping speed are all independent of body size, scaling with the -0.11 , 0.04 and 0.018 powers of body mass, respectively. Therefore, at all of the equivalent speeds except the minimum trotting speed, the amount of energy expended by each kilogram of animal to sustain a constant speed along the ground is directly proportional to the stride frequency used by the animals, and the energy expended per gram per stride is the same in all the animals.

Cost per kilogram per stride versus body mass

Why is the energy cost per kilogram per stride nearly the same at equivalent speeds over the entire size range of animals, despite the large differences in speeds, frequencies and energy costs? It seems reasonable to assume that the same volume of muscle relative to body mass is active at these speeds in different-sized mammals. The average force that is applied to the ground by the limbs over an integral number of strides is approximately equal to the body mass of the animal, i.e. the force per gram is the same for all animals (Cavagna *et al.* 1977). The force that a given cross-sectional area of muscle develops at equivalent points on the force-velocity and tension-length relationships is also about the same, suggesting that equivalent volumes of muscles relative to body mass will be required to generate equivalent forces on the ground. This is consistent with the observation that muscles make up 40–45 % of body mass in all mammals (Schmidt-Nielsen, 1984).

If the same relative volumes of muscles are active at equivalent speeds, then our results would indicate that the rate of energy consumption per kilogram of active muscle is directly proportional to the stride frequencies used by different-sized animals at each of these speeds. Two processes contribute to the energy consumption of active muscle: an activation cost (i.e. the cost associated with pumping calcium into the sarcoplasmic reticulum, accounting for about 30 % of the total cost) and a force-generation cost (the cost associated with the cycling of the cross-bridges between actin and myosin, accounting for about 70 % of the total; Rall, 1986). It seems reasonable to expect that the cost of activation will vary directly with stride frequency because the muscles will be turned on and off once per stride. It also seems reasonable to expect that the cost of force generation will vary directly with stride frequency at equivalent speeds in the different animals. The same average mass-specific force will have to be generated and decay once during each stride. However, the higher stride frequencies of the smaller animals require faster rates of force generation and decay, and this in turn requires faster

rates of cross-bridge cycling. Thus the cost of generating the same average force over an integral number of strides will increase directly with the stride frequency of the different-sized animals. A recent study in which isolated mammalian muscles were stimulated and shortened in a manner that mimics the muscular events occurring during locomotion supports this interpretation of why the cost of generating force increases with stride frequency. Heglund & Cavagna (1987) found that the cost of generating force per kilogram for a second is proportional to the rate with which the force is generated and decays (i.e. the intrinsic velocity of shortening), and appears to be independent of the work performed by the muscle.

Cost per kilogram per stride versus speed

Why does the energy cost per stride increase with speed? One possibility is that this increase is due to a change in the mechanical advantage of the limbs, requiring a greater muscular force for the same ground reaction force. In both a trot and a gallop, stride length during the time the foot is in contact with the ground increases with speed, thus the limb excursion angle increases with increasing stride length. This increase will change the average mechanical advantage between the limb muscles and the ground and will require that a greater average muscle force be developed. Thus, although the average ground reaction force over an integral number of strides does not increase with speed, muscle force will increase.

Within a trot, the rate of energy consumption doubles while the stride frequency increases by only 1.6-fold. Thus cost per stride increases by 25 % over the 2.6-fold increase in trotting speed. The increase in stride frequency almost, but not quite, matches the increase in rate of energy consumption. Three-quarters of the increase in cost with speed could be explained by the higher costs associated with higher stride frequencies. The remaining quarter might be explained by increasing average muscle force associated with increasing stride length. However, other factors might also be involved. For example, the muscles may be operating on different parts of their force-velocity and force-length relationships, requiring a greater volume of muscle for the same force generation; the relative importance of elastic storage and recovery of energy may decrease; and so on.

In a gallop the situation is more extreme. Stride frequency increases only by 10 %, and increasing stride length accounts for almost all the two-fold increase in speed. Thus mechanical advantage will change much more dramatically and the higher average muscle force this entails might contribute more significantly to the approximate doubling in the cost per kilogram per stride within this gait.

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