

Review

Similarity in multilegged locomotion: Bouncing like a monopode

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Abstract. Despite impressive variation in leg number, length, position and type of skeleton, similarities of legged, pedestrian locomotion exist in energetics, gait, stride frequency and ground-reaction force. Analysis of data available in the literature showed that a bouncing, spring-mass, monopode model can approximate the energetics and dynamics of trotting, running, and hopping in animals as diverse as cockroaches, quail and kangaroos. From an animal's mechanical-energy fluctuation and ground-reaction force, we calculated the compression of a virtual monopode's leg and its stiffness. Comparison of dimensionless parameters revealed that locomotor dynamics depend on gait and leg number and not on body mass. Relative stiffness per leg was similar for all animals and appears to be a very conservative quantity in the design of legged locomotor systems. Differences in the general dynamics of gait are based largely on the number of legs acting simultaneously to determine the total stiffness of the system. Four- and six-legged trotters had a greater whole body stiffness than two-legged runners operating their systems at about the same relative speed. The greater whole body stiffness in trotters resulted in a smaller compression of the virtual leg and a higher natural frequency and stride frequency.

Key words: Legs – Locomotion – Stiffness – Energetics – Mechanics

Introduction

Millions of years of evolution have resulted in a large number of locomotory designs that all seem to be satisfactory for the habitat of the respective animal. For example, major variation is observed in: 1) the *number* of legs used – from two in humans to about two hundred in a millipede; 2) the *length* and *shape* of legs – some spiders possess extremely long and slender legs whereas hedge-

hogs have comparatively short legs; 3) the *positioning* of the legs – insects carry their body between the legs, whereas mammals tuck their legs underneath; and 4) the type of *skeleton* – arthropods use an exoskeleton made of chitin-protein cuticle, whereas vertebrates use an endoskeleton composed of bone.

Despite this diversity, legged locomotion in most animals is accomplished by moving a skeletal linkage with the aid of muscles. Recent investigations have revealed a striking similarity in the general energetics and mechanics of legged animals during locomotion. This similarity is seen in:

1) *Metabolic energetics:* The minimum cost of locomotion for over one hundred and fifty animals that differ in leg number, skeletal type and body form follows a single function (Full 1991). Birds and mammals (Taylor et al. 1970), reptiles (John-Alder et al. 1986), amphibians (Full et al. 1988) and arthropods (Full et al. 1990) use less energy to move a unit mass of their body a unit distance if they are large.

2) *Gait:* Animals of very different design can use similar gaits (Hildebrand 1976). Many species can use a regularly symmetrical alternating gait (e.g., a trot). Two sets of propulsors are used, one after the other. The set can differ in the number of legs used (e.g., one for a human, two for a dog, three for a cockroach and four for a crab). Inverted-pendulum walking gaits and spring-like bouncing gaits have been found in diverse species from crabs to dogs (Blickhan and Full 1987; Cavagna et al. 1977; Full 1989; Heglund et al. 1982). Measurement of skeletal strain in quadrupedal mammals (Biewener and Taylor 1986) and crabs (Blickhan et al. 1993) support the hypothesis of equivalent gaits (Alexander 1989).

3) *Stride frequency:* Stride frequency at equivalent gait transitions (e.g., trot-gallop) decreases with an increase in body mass in quadrupedal mammals (Heglund et al. 1974; Heglund and Taylor 1988). Blickhan and Full (1987) discovered that ghost crabs change gait from a trot to a gallop at the same stride frequency and speed as a mouse of a similar size. Cockroaches follow similar

trends if frequency and speed relationships of gait transitions are extrapolated to smaller animals (Full and Tu 1990, 1991; Full 1989, 1991).

4) *Ground reaction force patterns*: Two-, four-, six-, and eight-legged animals can produce qualitatively similar ground-reaction force-patterns (Full 1989, 1991). One step of a propulsive system in a bouncing gait is characterized by a rise and fall in the vertical force concomitant with a deceleration followed by an acceleration in the horizontal direction.

5) *Mechanical energetics*: Legged animals investigated thus far generate about the same amount of mechanical energy to move a unit of their body mass a unit distance (i.e., 1 [J kg⁻¹m⁻¹]; Blickhan and Full 1987; Full 1989, 1991; Full and Tu 1990, 1991; Heglund et al. 1982). The mechanical energy of transport is derived from the fluctuations of the energy of the center of mass (Blickhan and Full 1992).

The remarkable similarities in energetic and mechanical parameters demand that there must be correspondence in the operation of musculo-skeletal systems. At present, however, we are uncertain as to how general a model of terrestrial locomotion can possibly be. Fortunately, several spring-mass models have been developed as a starting point (Blickhan 1989a,b; McGeer 1990; McMahon 1985; McMahon and Cheng 1990; Raibert et al. 1986). Blickhan (1989b) applied his spring-mass model in a comparison of bipedal runners and hoppers and found surprising similarities in the force exerted per leg, the relative compression of the legs, and the sum of the total energy fluctuations of the center of mass. To further elucidate similarities in energetics and mechanics, we use data available in the literature to investigate leg function in diverse species of animals. We use the spring-mass model of Blickhan (1989a) to test the hypothesis that the dy-

namics of legged locomotion in bipeds and polypeds that trot, run or hop can be explained by a monopode consisting of a massless spring attached to a point mass.

Model and parameters

The virtual monopode. We consider here only gaits whose dynamics might be reasonably described by a bouncing monopode. Slow gaits which do not include bouncing such as walking, crawling or metachronal gaits where action of the total system can not be described by a spring-mass system are excluded from this comparison. The same is true for galloping where the interaction of the movement of the body with the movement of the legs must be included for reasonable modeling. However, in a number of gaits the action of many legs and part of the body may be suitably modeled by a single massless spring (McMahon 1985; Blickhan 1989a; McMahon and Cheng 1990). This spring with a point-mass attached to it, representing the total mass of the animal is termed the virtual monopode.

Spring-mass model. The dynamics of a bouncing monopode depend on the angle of attack of the spring and the spring's stiffness. The angle of attack is directly related to the ratio of the horizontal and vertical component of the ground reaction force ($F_x F_y^{-1}$; Blickhan 1989a,b). To estimate the stiffness of the monopode, simultaneous measurements of the force acting on the spring and the spring's compression are required. The ground reaction force generated by the monopode is equivalent to the vector of the total force generated by all legs simultaneously and can be obtained from typical force tracings published by various investigators (see Table 1). At midstance, horizontal forces vanish and only the vertical component (F_y) need be considered. At first glance, it appears as if the compression of the spring could be calculated from the fluctuations of the potential energy of the center of mass that is proportional to its vertical displacement (Δy ; Fig. 1). The vertical displacement, however, is not equal to the compression of the spring (Δl ; Blickhan 1989a; Fig. 1). Based on a few kinematic or dynamic parameters the fluctuations of the mechanical energy of the center of mass can be predicted correctly for a human runner or hopper (Blickhan 1989a). In reverse, it is proposed here that for gaits which can be modelled by a bouncing monopode the compression of its spring can be easily

Table 1. Trotters, runners and hoppers used in monopode analysis

Gait	Common name	Species	Mass [kg]	Stride frequency [s ⁻¹]	Speed [ms ⁻¹]	References
Trot	Cockroach	<i>Blaberus discoidalis</i>	0.0025	11.10	0.36	Full and Tu (1990)
	Crab	<i>Ocypoda quadrata</i>	0.052	5.56	0.76	Blickhan and Full (1987)
	Dog	<i>Canis familiaris</i>	17.5	2.27	3.50	Cavagna et al. (1977)
	Ram	<i>Ovis musimon</i>	85	1.57	1.66	Cavagna et al. (1977)
Run	Painted quail	<i>Excalfactoria chinensis</i>	0.042	4.57	1.04	Heglund et al. (1982)
	Bobw. quail	<i>Colinus virginianus</i>	0.164	3.94	2.25	Heglund (pers. comm.)
	Bobw. quail	<i>Colinus virginianus</i>	0.176	3.56	1.49	Heglund (pers. comm.)
	Bobw. quail	<i>Colinus virginianus</i>	0.176	4.80	1.75	Heglund et al. (1982)
	Turkey	<i>mellegria gallopavo</i>	7	2.11	3.75	Cavagna et al. (1977)
	Rhea	<i>Rhea americana</i>	22.5	2.20	4.69	Cavagna et al. (1977)
	Human	<i>Homo sapiens</i>	65	1.34	3.97	Cavagna et al. (1977)
Hop	Kangaroo-rat	<i>Dipodomus merriami</i>	0.035	7.24	1.76	Heglund et al. (1982)
	Kangaroo-rat	<i>Dipodomus spectabilis</i>	0.1	5.32	1.39	Heglund (pers. comm.)
	Kangaroo-rat	<i>Dipodomus spectabilis</i>	0.1	6.32	2.12	Heglund et al. (1982)
	Springhare	<i>Pedetes cafer</i>	2.5	2.94	4.30	Cavagna et al. (1977)
	Kangaroo	<i>Megaleia rufa</i>	20	2.27	6.77	Cavagna et al. (1977)
	Kangaroo	<i>Megaleia rufa</i>	20	2.06	2.83	Cavagna et al. (1977)

Data available from publications and personal communications (Forces are found in Table 2)

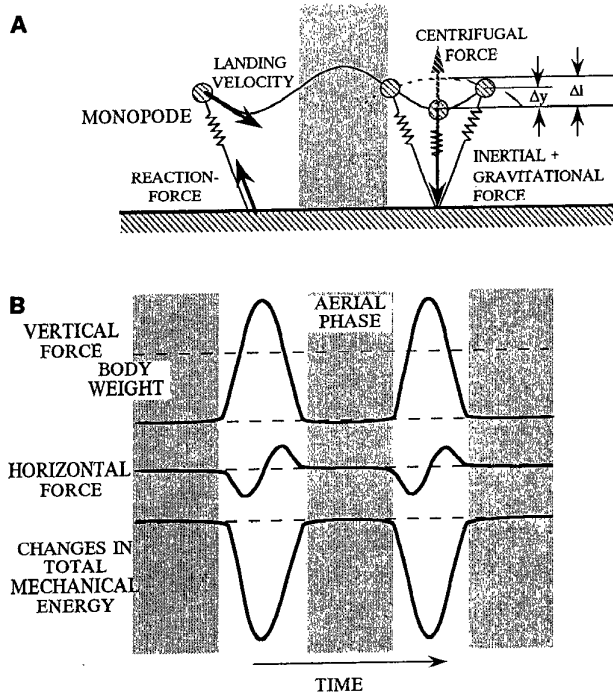


Fig. 1. **A** The bouncing monopode as model. Compression of the virtual leg (Δl) is different from the vertical oscillation of the center of mass (Δy). **B** Ground-reaction force and energy pattern observed for running, trotting, and hopping animals. During the aerial phase the total energy of the center of mass does not change, whereas it decreases during ground contact

calculated from the tracings of the total energy of the center of mass (E_{tot} ; Figs. 1 and 3; Cavagna et al. 1964; Cavagna 1975):

$$E_{tot} = E_{pot} + E_{kin,y} + E_{kin,x} + E_{kin,z}, \quad (1)$$

where E_{pot} is the change in potential energy and $E_{kin,y,x,z}$ represents the kinetic energy in vertical, horizontal and lateral directions, respectively.

In a bouncing monopode E_{tot} remains constant during the aerial phase. During ground contact the total energy decreases due to the simultaneous reduction of potential and kinetic energy. The decrease in total energy is equal to the work done on the monopode (ΔW) during each ground contact which in turn is equal to the product of force at midstance (F) times one half the compression (Δl) of the leg of the virtual monopode:

$$\Delta E_{tot} = \Delta W = \frac{1}{2} F \Delta l. \quad (2)$$

Here a linear relationship between force and displacement has been assumed which is in good agreement with experimental findings (McMahon and Cheng 1990).

The decrease in total energy at each bounce (ΔE_{tot}) can be estimated from the sum of the positive fluctuations in total power of the center of mass (P_{tot} ; as given in the literature) by dividing P_{tot} by step frequency (f_{step}). We calculated the compression of the monopode's leg (Δl) by dividing ΔE_{tot} by the ground reaction force:

$$\Delta l = 2 P_{tot} f_{step}^{-1} F^{-1}. \quad (3)$$

Force and mechanical energy data. Our comparison is limited by the number of ground reaction force tracings available in the literature that can serve as source data (Table 1). From the force tracings, we estimated peak vertical force at midstance (F). The energetics of the center of mass (E_{tot}) has been measured for relatively few species. From the regressions given for the specific rate of external mechanical work we obtained the total mechanical power at the respective

speed which divided by the stride frequency yielded an estimate of E_{tot} (see Blickhan and Full 1987, for revision of the data published by Heglund et al. 1982; Full and Tu 1990, 1991; Full 1989, 1991).

Model parameters. Given our estimates of force (F) and compression of the leg (Δl), we calculated the stiffness of a virtual monopode's leg for each species. Almost linear force-displacement relationships have been found for human hoppers (Farley et al. 1991) and kangaroos (McMahon 1990) corresponding to the assumption of a constant stiffness. Given the gait and number of legs used, we also determined the force per leg and the average contribution of each leg to the stiffness of the monopode. However, to accomplish these comparisons of animals as different as cockroaches and kangaroos, we found it helpful to introduce dimensionless quantities. We normalized forces to body weight (i.e., $F mg^{-1}$). We attempted to normalize the compression of the leg to either the length of the monopode leg or to the length of the animal's leg. Since neither of these lengths were available for each animal, we assumed geometrical scaling of leg length (Alexander 1988) and normalized with respect to this quantity (i.e., $\Delta l l^{-1}$). By dividing the relative force by the relative compression of the spring we calculated the relative stiffness (k_{rel}) of the monopode's leg

$$k_{rel} = \frac{\frac{F}{mg}}{\frac{\Delta l}{l}}. \quad (4)$$

Relative stiffness must be similar if animals are bouncing in a dynamically similar fashion (Blickhan 1989a). This results from the constraint that the ratios of the centrifugal force and body weight as well as the natural frequency and angular velocity during ground contact must be similar (Fig. 1):

$$\frac{\text{centrifugal force}}{\text{weight}} = \frac{\frac{mv^2}{l}}{mg} = \text{constant}_1, \quad (5)$$

$$\frac{\text{natural frequency}}{\text{angular velocity}} = \frac{\omega}{\frac{v}{l}} = \text{constant}_2, \quad (6)$$

with the stiffness of the monopode's leg

$$k = \frac{F}{\Delta l} \quad (7)$$

and

$$\omega^2 = \frac{k}{m}. \quad (8)$$

Substitution (solving Eqs. 4 and 5 for ω and Eq. 6 for k and substituting into Eq. 7) results in the condition that

$$k_{rel} = \frac{\frac{F}{mg}}{\frac{\Delta l}{l}} = \text{constant}.$$

The relative stiffness is identical to the dimensionless length (l_s) introduced as a characteristic parameter in the differential equations describing the dynamics of the spring-mass system during ground contact (Blickhan 1989a). In a similar way the Reynolds number is a dimensionless parameter in the differential equations describing flow in fluids.

Bouncing systems can only bounce in a dynamically similar way if they are loaded under comparable initial conditions. These initial conditions are specified by the angle of attack of the spring, a quantity not investigated in the present paper (comp. Farley et al. 1993), and the vector of the landing velocity of the center of mass. The horizontal component of this vector can be approximated by

the speed of locomotion (v) which in the dimensionless formulation of the differential equations (Blickhan 1989a) is defined as

$$v_{\text{rel}} = \frac{v\omega}{g}. \quad (9)$$

The corresponding vertical component, not considered here has been introduced in the description of the vertically bouncing monopode as "Groucho number" (McMahon et al. 1987). Similar relative velocities (v_{rel}) guarantee, together with the angle of attack, comparable loading conditions for animals of different size running at different speeds.

The natural frequency of the spring mass system. We calculated the natural frequency of an animal's spring-mass system ($f = \omega / 2\pi$) in two ways. First, we determined f_k by using the total energy fluctuations of the center of mass (ΔE_{tot} ; i.e., the method described above). Second, we estimated f from the width of the ground-reaction force tracings ($t(\text{mg})$) at the level of body weight ($f_{t(\text{mg})}$; Fig. 1). For the limit of vertical bouncing (one degree of freedom) this duration of time represents about half the period of the spring-mass system. For planar systems $t(\text{mg})$ corresponds rather well to the halfperiod of the vertical component of the spring-mass system, which can be calculated from the vertical displacement of the center of mass and the ground reaction force (Cavagna et al. 1988), it does not correspond to the halfperiod of the actual spring stiffness of the leg which is related to f_k .

In a spring-mass system with two degrees of freedom vertical and horizontal forces are interdependent (Blickhan 1989a) and considerable deviations from a single sinus-function symmetrical with respect to body weight (mg) can occur in the time course of the vertical force (Fig. 2). Obvious deviations in the shape of the force tracings are observed if the horizontal force becomes higher than the vertical component. High horizontal forces can be achieved by a large angle of attack (α) of the spring combined with high speed loading. This is rarely observed as it would require an unusually strong foothold (Blickhan 1989a). For the investigated data ($F_x \leq 0.27 F_y$) the differences are less pronounced but not negligible. From model studies it can be deduced that depending on the ratio between the vertical (u_y) and horizontal (u_x) component of the landing velocity the ratio between $f_{t(\text{mg})}$ and f_k can reach the value of 2. For the observed force ratios the following approximation can be deduced for this frequency ratio termed relative frequency (f_{rel}):

$$f_{\text{rel}} = \frac{f_{t(\text{mg})}}{f_k} = 1 + 0.1 \frac{u_x}{u_y}. \quad (10)$$

In our investigation u_x/u_y is less than 10. For animals of different size bouncing in a dynamically similar way this ratio should be similar. For forward bouncing systems the frequency ratio should be significantly larger than 1, i.e., the system should be stiffer in the vertical direction, and equation 10 should largely predict its value. If the monopode describes the kinetics of the system then the difference between the natural frequency of the vertical and the total spring can be largely explained from the horizontal and vertical components of the landing velocity (Eq. 10) and the ratio (f_{rel}) between the relative frequency measured and its value predicted by Eq. 10 should be 1.

Gaits and leg number. Since dynamics may depend on gait and leg number, we defined trotters, runners and hoppers and the numbers of legs they use. Bipeds that move their legs out of phase were considered runners, whereas those that move their legs in phase were hoppers. Hoppers and runners use two legs and mammalian trotters use four (alternating biped). Crabs and cockroaches are also trotting at intermediate speeds, i.e. they move diagonal legs synchronously. From our own observations, we found that crabs only use six legs (alternating tripod) instead of eight during trotting (Blickhan and Full 1987) as do cockroaches (Full and Tu 1990).

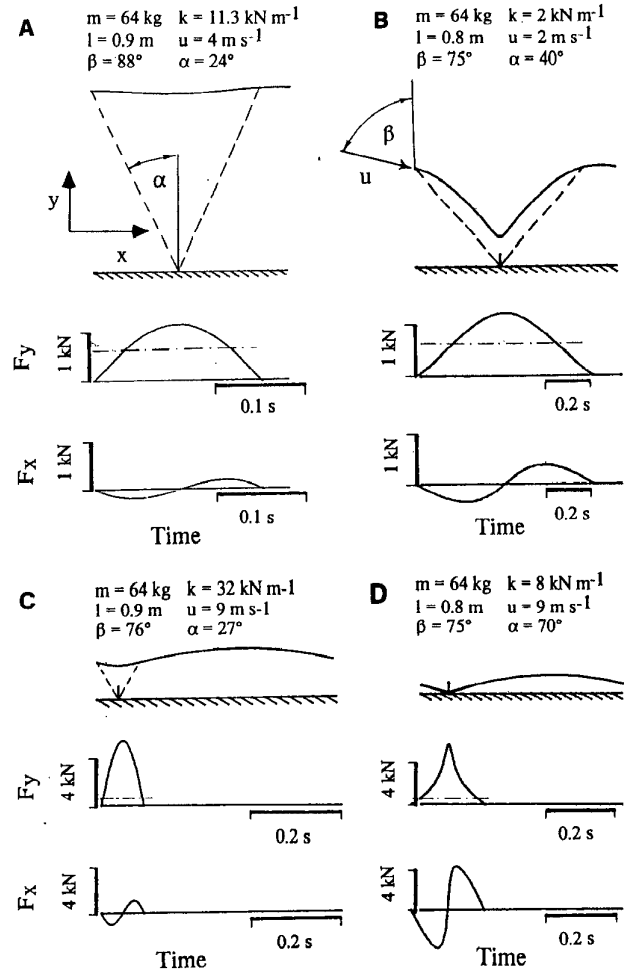


Fig. 2A–D. Path of the planar monopode and the time course of the ground reaction force during one complete step as obtained from numerical simulations. **A** Slow run with low vertical landing velocity. The time course of the force tracing is not similar to a sine wave symmetrical to mg ($f_{\text{rel}} = 1.9$; $k_{\text{rel}} = 8$). **B** Running on a soft spring. The dominance of the spring's compression results in a more sinusoidal time course of the ground reaction force ($f_{\text{rel}} = 1.1$; $k_{\text{rel}} = 2.6$). **C** Fast hop. Even though the force seems to approach a sinus half-wave $t(\text{mg})$ is reduced due to the action of centrifugal forces ($f_{\text{rel}} = 1.6$; $k_{\text{rel}} = 46$). **D** A low angle of attack or large α results in a modified time course of the force ($f_{\text{rel}} = 1.6$; $k_{\text{rel}} = 10$).

List of variables

E ,	sum of positive increments in energy of the center of mass
f ,	natural frequency
$F = F_y$,	ground reaction force at midstance
F_r ,	Froude number
F_x, F_y ,	peak ground reaction force components
k ,	stiffness
l ,	length of the leg of the virtual monopode
m ,	mass
v ,	running speed
u ,	landing velocity
ΔW ,	work during ground contact
Δl ,	compression of the virtual leg
ω ,	natural cycle frequency
α ,	angle of the spring with respect to the vertical
β ,	angle of u with respect to the vertical
σ ,	Strouhal number

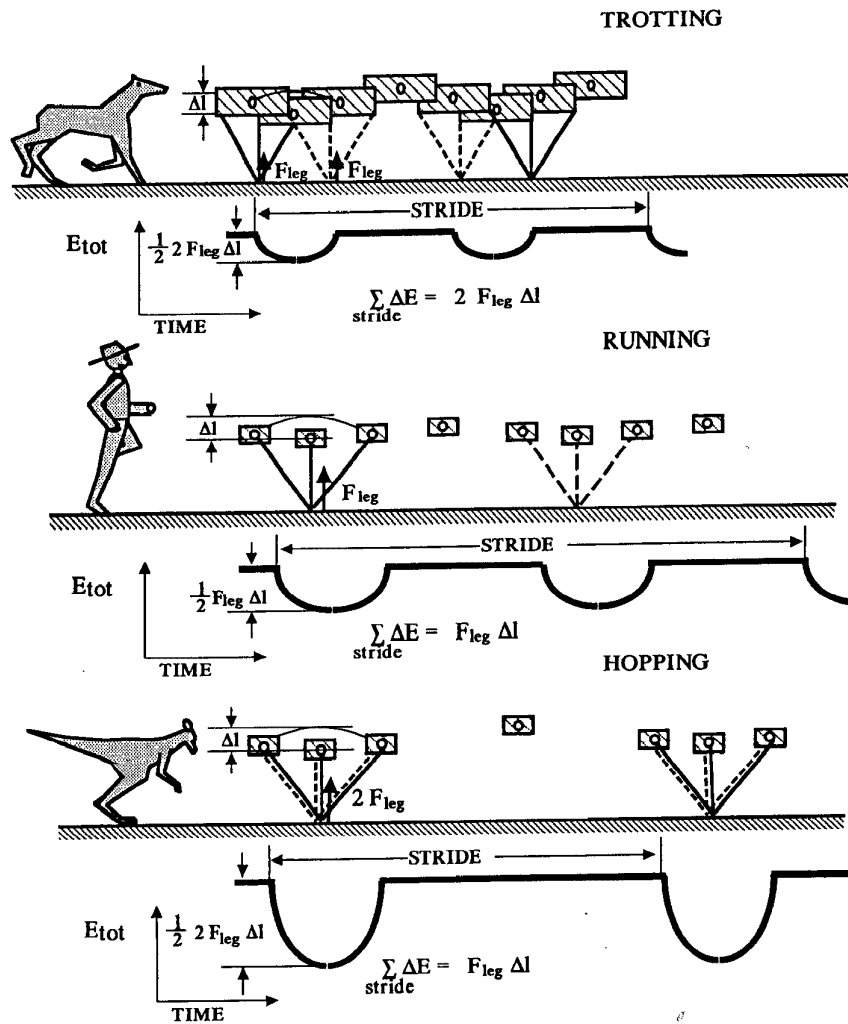


Fig. 3. Motion of the center of mass and time course of total energy of the center of mass for a trotting, running, and hopping monopode model. The amount of the fluctuation in energy (E_{tot}) can be calculated from the ground-reaction force per leg (F) and the compression of the spring (Δl). Dashed lines indicate legs in ground contact with the ground on the left side of the animal. Work done per stride by a four-legged trotter is equal to the sum of $\frac{1}{2} F \Delta l$ for two legs and two steps. Work done per stride by a bipedal runner is equal to the sum of $\frac{1}{2} F \Delta l$ for one leg and two steps. Work done per stride by a bipedal hopper is equal to the sum of $\frac{1}{2} F \Delta l$ for two legs and one step

Suffixes

k,	calculated from stiffness and E
leg,	per leg
rel,	relative
t,	calculated from the time course of the ground reaction force
tot, pot, kin,	total, potential, kinetic
vert,	vertical
x,y,z,	horizontal, vertical, lateral

Results

Ground-reaction force

The peak magnitude of the relative ground-reaction force ($F mg^{-1}$) is an indicator of the fraction of time an animal spends on the ground, and thus is a suitable first indicator of dynamic similarity for a bouncing monopode (Blickhan 1989a). Variation of the relative ground-reaction force ranged from 1.3 for a cockroach to 6.0 for a hare (Table 2). The relative ground-reaction force during each bounce was gait dependent. Hopping was dynami-

cally distinct from running and trotting. Ground-reaction forces for trotters (range 1.3 to 2.2, cockroach to crab) were lower than those observed in runners (2.2, quail and 2.5, quail). Hoppers produced significantly higher ground-reaction forces (3.8, kangaroo-rat and 6.0, hare; Blickhan 1989b) than trotters and runners.

We found an even greater variation in the relative force per leg (cockroach: 0.4, hare, 3.0; Table 2; Fig. 4A), since ground-reaction forces in trotters are generated with a different number of legs. Force per leg depended on the gait and the number of legs used during ground contact. The lowest force per leg was found in six-legged trotters (cockroach, 0.4), followed by quadrupedal trotters (dog, 1.1), and bipedal hoppers and runners (kangaroo rat, 2.0; hare, 3.0; quail, 2.2; man, 2.8). Force per leg was similar for runners and hoppers (Blickhan 1989b), but considerably lower for trotting animals.

Compression of the leg of the virtual monopode

The relative compression of the legs ($\Delta l l^{-1}$) differed by a factor of 5 between various animals. Shortening of the

Table 2. Dimensionless parameters for trotting, running, and hopping

	Polypeds			Bipeds					
	Trot \bar{x}	S.D.	Trot-run P	Run \bar{x}	S.D.	Run-hop P	Hop \bar{x}	S.D.	Hop-trot P
$F \text{ mg}^{-1}$	1.78	0.37	≤ 0.05	2.26	0.13	≤ 0.0005	5.06	0.79	≤ 0.0005
$F \text{ mg}^{-1} \text{ leg}^{-1}$	0.78	0.29	≤ 0.0005	2.26	0.13	> 0.05	2.54	0.39	≤ 0.0005
$\Delta l \text{ l}^{-1}$	0.096	0.020	≤ 0.0005	0.243	0.056	> 0.4	0.237	0.071	≤ 0.005
k_{rel}	18.60	1.68	≤ 0.0005	9.76	2.44	≤ 0.0005	22.20	4.21	> 0.05
$k_{\text{rel}} \text{ leg}^{-1}$	7.82	2.26	> 0.1	9.76	2.44	> 0.1	11.10	2.10	≤ 0.025
v_{rel}	4.02	1.87	> 0.1	5.33	1.30	≤ 0.005	9.95	2.84	≤ 0.005
f_{rel}	1.59	0.28	≤ 0.05	1.92	0.22	≤ 0.05	1.59	0.26	> 0.4
f_{rat}	1.11	0.16	> 0.1	1.16	0.17	> 0.4	1.18	0.14	> 0.1

\bar{x} represents mean; S.D. is one standard deviation; P represents level of significance (ANOVA and post hoc test)

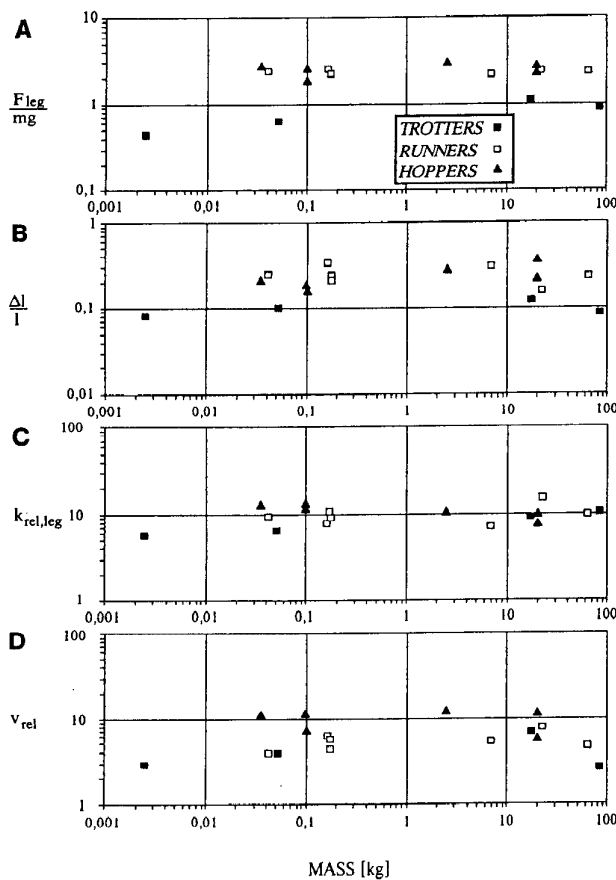


Fig. 4A–D. Dimensionless parameters of the monopode model for trotters, runners and hoppers as a function of body mass. All parameters changed less than half a decade over a mass range of four to five-fold. $F \text{ mg}^{-1}$ is the relative ground reaction force; $\Delta l \text{ l}^{-1}$ is relative leg compression, $k_{\text{rel,leg}}$ is relative leg stiffness, v_{rel} is relative velocity

virtual monopode leg was gait dependent (Table 2), but did not depend on size. The compression was significantly smaller for trotters (cockroach, 0.078; dog, 0.122) than runners or hoppers, but did not differ between bipedal runners (quail, 0.24; turkey, 0.30) and hoppers (kangaroo rat, 0.16; kangaroo, 0.36; Fig. 4B).

Stiffness

Relative whole body stiffness calculated from the energetics of the center of mass ranged from 7.1 (turkey) to 25.6 (kangaroo rat). The stiffness of the monopode leg depended on the gait of the animal (Table 2). Values for runners (turkey, 7.1; rhea, 14.5) were significantly lower than for trotters and hoppers (kangaroo, 15.4; kangaroo rat, 27.2; cockroach, 16.7; ram, 20.7) whose values did not differ.

Stiffness per leg

Despite differences in locomotory style, the contribution of each leg to stiffness appeared to be rather similar (Fig. 4C). Relative stiffness per leg showed a smaller variation (i.e., from 5.6 to 14.6) than whole body stiffness (Table 2). Analysis of variance revealed only a weak dependence on leg number ($P \leq 0.07$) and gait ($P \leq 0.04$). In trotters these values ranged from 5.6 (cockroach) to 10.4 (ram), in runners from 7.1 (turkey) to 14.6 (rhea), and in hoppers from 7.7 (kangaroo) to 13.6 (kangaroo-rat).

Speed

Differences in gait dynamics are also due to differences in the loading conditions indicated by the values obtained for the relative speed (ram, 3.7; dog, 9.5; quail, 5.5; rhea: 10.9, kangaroo, 8.0; spring hare, 17.5; Fig. 4D). Relative velocities were significantly greater in hoppers compared to runners and trotters (Table 2).

Natural frequency of the spring mass system

The ratio of natural frequency calculated by two methods ($f_{\text{rel}} = f_{\text{t(mg)}} f_{\text{k}}^{-1}$) was our least variable quantity (i.e., ranged from 1.2 to 2.1). It was significantly different from 1 ($P < 0.001$), i.e. the use of $t_{\text{(mg)}}$ results in an overestimation of the actual natural frequency of the monopode by ca. 70% (Table 2). The ratio did not depend on size ($P > 0.9$) or leg number ($P \geq 0.1$). The ratio was significantly higher for runners (quail, 1.6; turkey, 2.0) compared to

trotters and hoppers (ram, 1.2; dog, 1.8; kangaroo, 1.2; kangaroo, 1.9). The magnitude of the relative frequency and its dependency on gait can largely be attributed to the different ratios of the horizontal and vertical components of the landing velocity, i.e. to the specific operation of the planar monopode: f_{rat} exceeds 1 only by 15% ($P < 0.005$; Fig. 4D), and no dependency on mass, leg number or gait can be verified ($P > 0.7$). By operating their system in a way which leads to a comparatively high vertical stiffness runners compensate for the larger relative compliance of their legs.

Discussion

General applicability of model

The monopode model appears to be very general and can aid in explaining the remarkable similarities in energetic and mechanical parameters seen in animals that differ in locomotor design. It represents a reasonable approximation of the dynamics used by many legged animals for terrestrial locomotion and it correctly predicts from initial conditions gait dependent differences. Likewise, variation resulting from differences in speed (Fig. 5) and body mass (Fig. 4) do not appear to prevent the discovery of the mechanical parameters that vary with locomotor design. Farley et al. (1993) have shown that leg stiffness is independent of speed in mammalian runners, trotters and hoppers. In the present study, most of the variation in relative force per leg, its compression and its stiffness can be attributed to specific gaits and not simply speed (Fig. 5).

The mass-specific mechanical energy used to move an animal's center of mass is independent of body mass (Blickhan and Full 1987; Cavagna et al. 1977; Full 1989, 1991; Heglund et al. 1982). Likewise, our analysis revealed that the relative vertical ground-reaction force and the relative compression of the leg of the virtual monopode did not depend on the animal's mass (Eq. 3; Fig. 4A,B). Yet, our analysis of the literature showed that these values differ depending on gait. Runners exerted about half the force of hoppers, but compressed their leg by a similar amount. Runners produced about twice as many steps as hoppers to cover a similar distance (Fig. 3). These differences in dynamics result in a similar energetics of the center of mass (Blickhan 1989b).

The ground-reaction force exerted by trotters was lower than that measured for runners and hoppers (Table 2). This admittedly small decrease was accompanied by a significantly smaller compression of the leg of the virtual monopode (Fig 4B; Table 2). Correspondingly, the work done on the monopode during landing was less for trotters than for runners. To a large extent, the decreased work on landing was compensated for by the distance covered during each step. The distance covered during trotting was only about half that measured for running, resulting in a higher step frequency and a more similar mechanical energy output of the center of mass. Perhaps, the higher step frequency in trotters is possible because of the lower mass of each leg in these multi-legged animals.

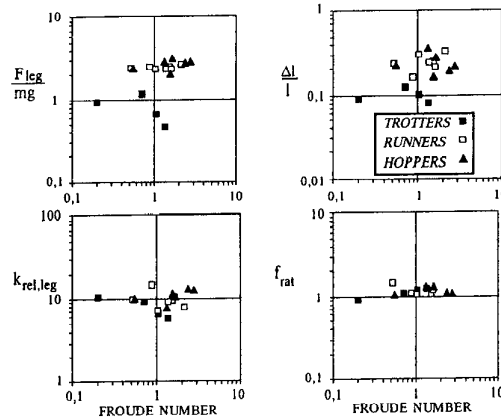


Fig. 5. The influence of speed on the investigated data. Most of the variance is due to the different gaits. Froude number = $\frac{v^2}{gl}$

This observation may be most relevant to the smallest trotters (i.e., cockroaches and crabs). Small trotters generated lower forces per leg (cockroach, 0.4) than runners and even large trotters (ram, 0.9; Fig. 4A; Table 2). Small animals distribute a similar force among a larger number of legs that may enable them to reduce the weight of an individual leg.

Stiffness of the virtual monopode

Relative whole body stiffness and relative speed of locomotion did not vary with body mass (Fig. 4C,D). This results in a decrease of the animal's natural frequency with body mass (since ω is proportional to the square root of length and length to the cube root of body mass; Blickhan 1989b):

$$f = \frac{1}{2\pi} \sqrt{\frac{k}{m}} = \frac{\omega}{2\pi} \propto l^{-\frac{1}{2}} \propto m^{-\frac{1}{6}} \propto m^{-0.166}. \quad (11)$$

The exponent predicted from the model was not significantly different from the scaling exponent found for the step-frequency of runners, trotters and hoppers. However, as for relative whole body stiffness, the value of step frequency differed greatly from gait to gait (i.e., the coefficient):

$$f_{\text{step,trot}} = (7.16 + 0.32/-0.21 \text{ SD}) m^{(-0.18 \pm 0.01 \text{ SD})} \quad (12)$$

$$f_{\text{step,run}} = (1.50 + 0.09/-0.09 \text{ SD}) m^{(-0.16 \pm 0.02 \text{ SD})} \quad (13)$$

$$f_{\text{step,hop}} = (3.74 + 0.12/-0.12 \text{ SD}) m^{(-0.19 \pm 0.01 \text{ SD})} \quad (14)$$

where the mass m is given in [kg] and the frequency f in [s^{-1}].

Relative whole body stiffness depended not only on gait, but also the number of supporting legs used (Table 2). Hoppers had twice the total relative stiffness of runners. Using two legs in synchrony allows hoppers to at-

tain long aerial phases resulting in a large relative speed (Blickhan 1989b). One might predict that runners and trotters achieve a similar gait by generating the same total stiffness with two alternating sets of legs. This was not the case. Stiffness per leg was not significantly lower in trotters and, thus, total stiffness was considerably higher (twice that of runners and more comparable to hoppers; Table 2). The same total force in trotters resulted in a much lower compression of the leg of the virtual monopode.

Especially in the smallest trotters like insects with crouched postures large vertical oscillations must be avoided to prevent contact with the substratum. This could be achieved by the observed high stiffness of the monopode. A more compliant monopode could minimize vertical oscillations by increasing its angle of attack, which in turn increases the vertical stiffness. This strategy is used by bipedal runners as indicated by the significantly higher horizontal forces ($F_x F_y^{-1}$: 0.10 ± 0.02 SD for trotters and 0.18 ± 0.06 SD for runners; $P \leq 0.025$) and the larger frequency ratio (f_{rat}). Disadvantages of this method are a reduced height of the center of mass above the ground and the necessity of stronger footholds. Low natural frequencies as observed in bipedal runners correlate with low step frequencies (Eqs. 12 and 13). This may reduce metabolic cost. On the other hand, especially for animals with a low hip height high step frequencies have an advantage with respect to dynamic stability because of the importance of minimizing falling time (Ting et al. 1990). For large mammals the observed differences between runners and trotters may reflect different strategies in motor-control. Trotters with high step frequency may specialize by a step by step adaptation to changing conditions. This facilitates control for systems where the kinetics of the monopode is determined by simultaneous action of several legs. Animals with low step frequencies may specialize on adjustments during a single ground contact.

Operation of single legs

Leg stiffness appears to be a very conservative quantity in the design of legged locomotor systems. Relative stiffness per leg was surprisingly similar in trotters, runners and hoppers (Fig. 4C; Table 2). An animal's whole body stiffness was in large part determined by the number of legs used.

Similarity in leg operation could mean that each leg functions in an identical fashion and contributes an equal amount of stiffness (McMahon 1985). In large runners and hoppers, stiffness can be simply related to the sum of the properties of individual legs. Dynamic legged robots that have two or four legs that all function alike operate in a similar manner (Raibert et al. 1986). In contrast, leg operation in insects, and perhaps other arthropods, does not show strict equivalence among legs.

Whole body stiffness can be determined by leg number without necessarily restricting each leg to function in an identical manner and without requiring each leg to provide an equal degree of stiffness. Our measurements in

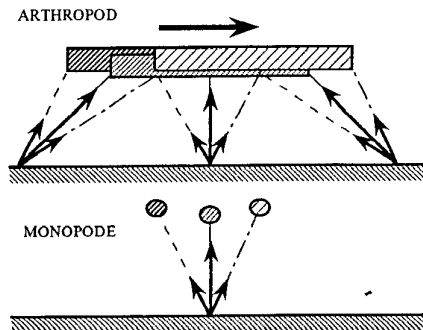


Fig. 6. In a trotting insect, all legs function to determine the characteristics of the virtual leg. Only the middle leg appears to be loaded as a monopode. The typical decelerating and accelerating pattern of a running monopode is observed and results in ground reaction forces directed towards the joints thereby reducing joint moments (Full et al. 1991)

cockroaches have demonstrated that during trotting, front and hind legs work against each other during a large fraction of the stride (Full et al. 1991). Each leg does not function as a virtual monopode. Only the middle legs shorten and lengthen symmetrically, while the front legs largely shorten during ground contact and the hind legs lengthen (Fig. 6). The decelerating and accelerating ground reaction-force pattern may be in part the result of a deviation from the strict alternating tripod pattern due to a sequential loading of the legs starting with the front leg and ending with the hind leg. An advantage of differential leg function may result in the minimization of joint forces, while still operating as a virtual monopode.

In conclusion, analysis of the present literature supported the hypothesis that a monopode model is a very general model of legged terrestrial locomotion and warrants further consideration. The model can allow a more quantitative comparison among diverse species than has been possible previously. Trotting can be compared to running and hopping, six-legged animals to two- and four-legged locomotors, and cockroaches to humans and kangaroos. Similarity in the operation of jointed framework skeletons is apparent, despite seemingly major differences in structure (e.g., endo- versus exoskeleton). In future analyses, departures from the model should prove as valuable as correspondence. We hope our analysis will encourage further tests of a monopode model and provide the ground work for the development of more comprehensive models of terrestrial locomotion.

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