

ANIMAL MOTILITY AND GRAVITY

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INTRODUCTION

In 1981 Pace and Smith (23) addressed the metabolic consequences of changes in gravity during rest or inactivity in animals. In this brief communication I will identify those variables that affect the metabolic cost of animal motility at 1G (G equals "times normal gravity") and those that are most likely to alter cost at higher and lower gravitational accelerations.

Our studies of the metabolic cost of terrestrial locomotion for a variety of small animals that appear to defy gravity (i.e. arthropods less than one gram in mass) show remarkable similarities to data collected for birds, mammals and lizards. At the onset of activity, the rate of oxygen consumption in many animals increases rapidly from resting to a steady-state. Below the maximum rate of oxygen consumption, steady-state rates represent the energy required for locomotion since non-aerobic pathways appear to contribute little energy. Steady-state oxygen consumption increases linearly with speed in two, four, six, eight, forty and even 100-legged runners (3).

MINIMUM COST OF LOCOMOTION AND SPECIFIC RESISTANCE

Differences in oxygen consumption become apparent when animals of different mass are compared. A gram of a small animal uses more energy per unit time to travel at a given speed than a larger animal. More importantly, smaller runners demand relatively more energy to increase speed. Likewise, they require relatively more energy to travel a given distance. The slope of speed versus steady-state oxygen consumption represents the minimum energy requirement per unit distance, termed the minimum cost of locomotion (28). The mass-specific minimum cost of locomotion in polyepedal runners decreases with an increase in body mass (9) and follows the same trend observed in two and four-legged runners (8, 12, 19, 26). To move a unit of mass one meter a three gram cockroach requires twice the energy of a 30 g crab or mouse and nine times that of a three kg dog.

The concept of the minimum cost of locomotion was actually borrowed from engineering. Gabrielle and von Karman (14) compared the economy of vehicles by determining a dimensionless ratio referred to as specific resistance. Specific resistance is the tractive force per unit weight or the amount of energy required to travel a given distance per unit weight and therefore includes a gravity term.

$$\text{Minimum Cost of Locomotion} = \frac{\text{Power input}}{\text{Velocity} \cdot \text{Body mass}}$$

$$\text{Specific Resistance} = \frac{\text{Power input}}{\text{Velocity} \cdot \text{Body mass} \cdot \text{Gravitational acceleration}}$$

The effect of gravity on specific resistance will depend on the degree to which the variables determining metabolic cost vary with alterations in gravity.

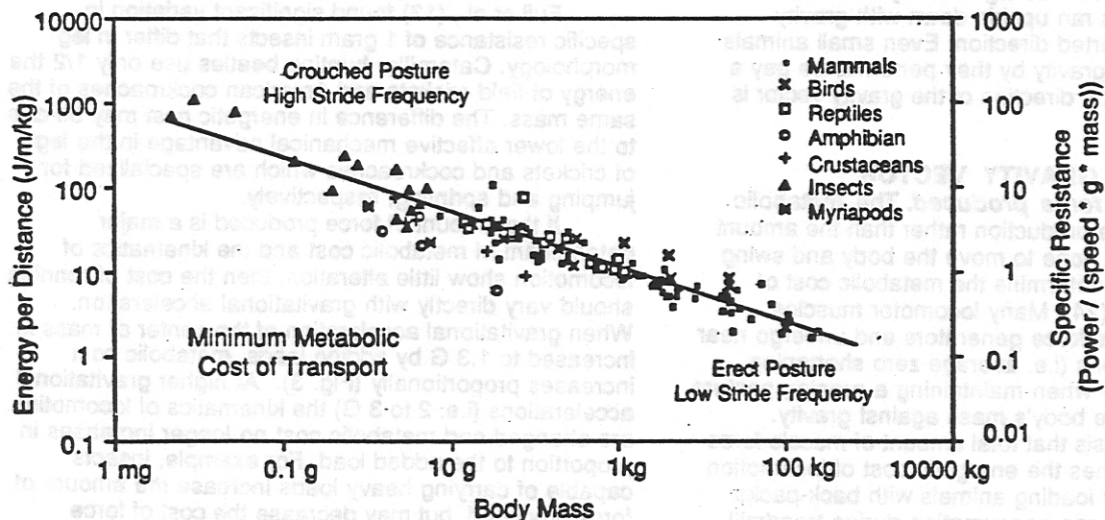


Fig. 1. Logarithmic plot of metabolic energy per distance or specific resistance as a function of body mass for over 150 different species studied by several investigators (see 9 for references).

DIRECTION OF GRAVITY VECTOR

It is well known that the direction of the gravity vector has a profound effect on large animals such as humans; climbing up and down hills or inclines increases energetic cost and the minimum cost of locomotion. Despite the fact that many small animals appear to scale surfaces effortlessly, energetic cost is increased. If the muscular efficiency of lifting a gram of body mass were a constant, small animals should require proportionally smaller increases in metabolic cost to run against gravity because their metabolic cost of locomotion per gram is much greater for level running than that of large animals (25; Fig. 1). The direction of gravity could have a minimal effect on the smallest animals.

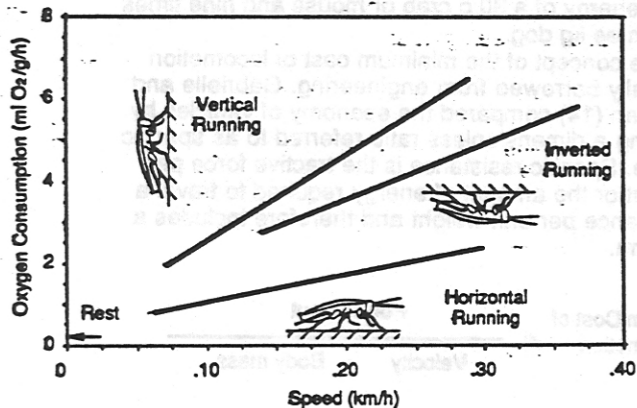


Fig. 2. Oxygen consumption as a function of treadmill speed for a cockroach (*Blaberus discoidalis*, 11).

Our study on small animals with an exceptional capacity for ascending steep gradients (i.e. 1 gram cockroaches) showed that the muscular efficiency of lifting a gram body mass is not necessarily a constant (11). The minimum cost of locomotion increased with an increasing angle of ascent; the minimum cost of locomotion was two and three times greater, respectively, at 45 and 90° inclines (Fig. 2). Likewise, the cost of locomotion was significantly increased when these small animals ran upside down with gravity operating in an inverted direction. Even small animals that appear to defy gravity by their performance pay a greater cost when the direction of the gravity vector is altered.

MAGNITUDE OF GRAVITY VECTOR

Amount of force produced. The metabolic cost of muscle force production rather than the amount of mechanical work done to move the body and swing the limbs may best determine the metabolic cost of animal locomotion (24). Many locomotor muscles function primarily as force generators and undergo near isometric contractions (i.e. average zero shortening velocity), especially when maintaining a running posture while supporting the body's mass against gravity.

The hypothesis that total amount of muscle force production determines the energetic cost of locomotion has been tested by loading animals with back-packs and measuring oxygen consumption during treadmill exercise (27) or measuring animals carrying natural loads like eggs (Fig. 3). Kinematic variables, such as acceleration of the center of mass and stride frequency, did not change when weight was increased by 10-30%. The increases in force exerted by anti-gravity muscles

was directly proportional to the mass of the loads carried. The increase in metabolic cost observed (loaded cost / unloaded cost) was directly proportional to the load carried (shown as G force) and therefore to the force exerted by anti-gravity muscles.

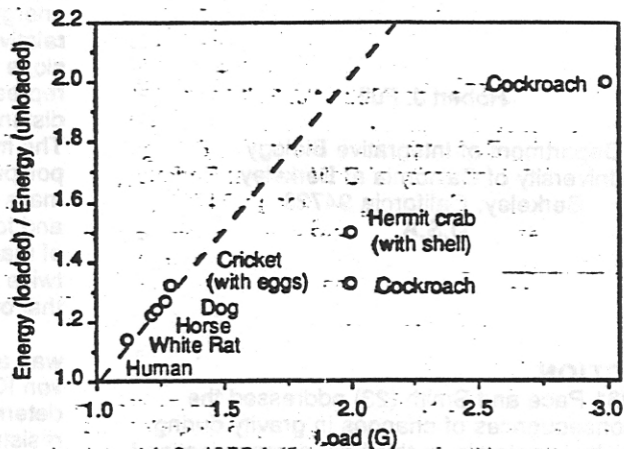


Fig. 3. Energy expended to carry a load at the center of mass relative to the energy expended carrying the body alone as a function of the load (shown as G). Dashed line represents a direct proportionality (e.g. 20% increase in load results in a 20% increase in cost) Data from 18, 27 and Full, unpublished.

If the force exerted by all anti-gravity muscles simply equals body weight, then the metabolic cost of locomotion in small and large animals should be the same per unit weight. Fig. 1 shows that assuming muscle force development is simply proportional to weight may be insufficient to explain the cost of locomotion. Because small mammals run in a more crouched posture, the effective mechanical advantage of their limb muscles can be 1/10 that of larger mammals (3). Small mammals weighing 0.3 N must generate 10 times as much muscle force to generate the same relative ground reaction force as larger mammals weighing 5000 N. Greater force production requires more metabolic energy.

Full et al., (13) found significant variation in specific resistance of 1 gram insects that differ in leg morphology. Caterpillar hunting beetles use only 1/2 the energy of field crickets and American cockroaches of the same mass. The difference in energetic cost may be due to the lower effective mechanical advantage in the legs of crickets and cockroaches which are specialized for jumping and sprinting, respectively.

If the amount of force produced is a major determinant of metabolic cost and the kinematics of locomotion show little alteration, then the cost of running should vary directly with gravitational acceleration. When gravitational acceleration of the center of mass is increased to 1.3 G by adding loads, metabolic cost increases proportionally (Fig. 3). At higher gravitational accelerations (i.e. 2 to 3 G) the kinematics of locomotion are changed and metabolic cost no longer increases in proportion to the added load. For example, insects capable of carrying heavy loads increase the amount of force produced, but may decrease the cost of force production by decreasing stride frequency. Changes in gravitational acceleration will produce alterations in the kinematics of running and affect the rate at which muscles must develop force to support the body's mass against gravity.

Rate of force development. - A change in the rate of muscle force development is a second important variable that may explain the relatively greater cost of locomotion in animals as they run faster, in small animals compared to large and in animals that have short legs or take relatively short steps (24).

By loading animals of different mass, Taylor et al., (27) found that the cost of force production may vary with body mass. Oxygen consumption rose in direct proportion to the added load for animals which ranged in mass from a rat to a horse. Since small animals have higher mass-specific metabolic costs for unloaded running (see Fig. 1), an equivalent increase in load or force produced a much greater increase in mass-specific metabolic cost in small animals compared to large. The development of each Newton of force by a small animal appears to require more metabolic energy than the development of the same amount of force by a large animal.

Small animals seem to require more metabolic energy to move a gram of body mass than larger ones because they must turn their muscles on and off more frequently per unit time or distance. The metabolic cost of force production varies with body mass in a similar manner to stride frequency. Higher rates of contraction appear to result in additional cost due to more frequent activation and the higher costs associated with the more rapid cycling of cross-bridges. When the metabolic cost of locomotion is normalized for the rate of force production, the mass-specific metabolic cost of locomotion for one stride is remarkably independent of body mass (16). Therefore, the greater metabolic cost per unit mass of small animals to travel a given distance could be explained by the fact that small animals, with shorter legs than larger animals, must take more steps costing an equivalent amount of mass-specific metabolic energy to cover the same distance.

The increase in metabolic energy with speed can also be explained by differences in the rate of force production. Depending on the gait employed, stride frequency and metabolic cost increase with an increase in speed. Normalizing metabolic cost for the rate of force production results in only a modest increase in the cost per stride as speed is increased (16). Kram and Taylor (20) suggested that normalizing for the rate of force production by using ground contact time may be more appropriate than dividing by stride frequency, because muscles are developing most of their force when the legs are in contact with the ground and are supporting the body's weight.

$$\text{Specific Resistance} = \frac{\sum \text{Muscle force}}{\text{Velocity} \cdot \text{Body mass}} \cdot \frac{\text{Cost of force production}}{\text{Gravitational Acceleration}}$$

$$\text{Specific Resistance} \propto \sum \text{Muscle force (weight supported, effective mechanical advantage)}$$

$$\text{Specific Resistance} \propto \frac{\text{Cost of force production}}{\alpha \cdot \text{cost coefficient} \cdot \text{Stride frequency}}$$

$$\alpha \cdot \text{cost coefficient} \cdot \frac{1}{\text{Contact time}}$$

Determinations of ground contact cost are remarkable similar over the range of sustainable speeds in insects (1.5 - 3.1 J kg⁻¹) to mammals (2 J kg⁻¹).

The rate of force production will depend on the kinematics of locomotion. Changes in gravitational acceleration have been shown to affect stride length, stride frequency and gait in humans (7, 21). The speed at which animals change from a walking gait to a

running gait appears to be a function of gravitational acceleration.

Two- and four-legged mammals, birds, and even eight-legged crabs use an energy conserving mechanism during walking that is analogous to an inverted swinging pendulum or an egg rolling end over end (5, 6, 15). By using this pendulum-like mechanism, kinetic energy and gravitational potential energy are exchanged, and not simply lost, as the animal's center of mass rises and falls during a stride. Vaulting over a relatively stiffened leg conserves up to 70% of the mechanical energy that must otherwise be provided by muscles and tendons.

A simple mathematical model has been used to explain how fast animals might walk using a pendulum-like energy exchange mechanism (1). The effective "hip" height of this inverted-pendulum arrangement is l , assuming the body moves on a pathway or arc of radius l . The body has an acceleration towards the supporting foot equal to the centrifugal force, u^2/l where u is speed. Since an animal does not pull itself downward, its acceleration cannot exceed the acceleration due to gravity, g . Maximum walking speed is therefore equal to $(gl)^{1/2}$. When gravitational acceleration decreases, maximum walking speed decreases, so as to be simply too slow (21). As found for astronauts on the moon, animals should change gait to a run or hop at lower speeds in reduced gravity.

A running or hopping gait is characterized by the time course of mechanical energy changes; kinetic and gravitational potential energy changes of the center of mass are in phase (6). Two-, four-, six- and eight-legged runners generate ground reaction force patterns that are remarkably similar and yield mechanical energy fluctuations that define a run or trot (9). Four-, six-, and eight-legged runners may have "equivalent" running gaits. At low speeds trotting dogs increase speed by increasing stride frequency. At high speeds stride frequency attains a maximum as dogs change from a trot to a gallop. Faster speeds are achieved by longer strides. This pattern is typical of four-legged mammals (17), eight-legged crabs (5) and six-legged insects (19) at the transition from a trot to a gallop or fast run. In mammals both the maximum sustainable stride frequency and the speed at which the maximum sustainable stride frequency is attained scale with body mass (17). A 30 g mouse changes from a trot to a gallop at a frequency twice that of 9 kg dog, but at speeds 1/4 as fast. Surprisingly, small cockroaches and eight-legged crabs follow the same trend toward increasing frequency with decreasing size, despite the striking diversity in morphology and physiology represented (9).

The hypothesis of dynamic similarity applied to terrestrial locomotion (2) predicts that animals of different size will run in a similar fashion whenever they have speeds proportional to the square roots of their effective leg length or hip height. Dynamic similarity is achieved when Froude numbers are equal, Froude numbers being the ratio of inertial to gravitational forces, u^2 / gl , where u represents speed, g is acceleration due to gravity and l is a general characteristic of length such as hip height. Four-, six- and eight-legged runners change gait as predicted by their Froude number at values of 2 - 3 (2, 5, 10).

The fact that ghost crabs and cockroaches change gait at almost the identical speed and stride frequency predicted for mammals of the same size suggests that spring-like systems based on similar muscle and connective tissue properties may be operating in terrestrial locomotion. Animals may very well operate as tuned mechanical spring systems possessing similar

spring-like properties (4, 22). To understand the dynamic adjustments animals make during locomotion at different gravitational accelerations, the variables of spring-mass models, such as effective vertical stiffness, leg stiffness and peak vertical force, must be examined. Investigators of locomotor dynamics (e.g. Thomas McMahon at Harvard University) have begun to test these models at different gravitational accelerations and make just such measurements.

SUMMARY

1. Specific resistance to locomotion will remain constant if changes in the amount of force produced or in the cost of force production are directly proportional to changes in gravitational acceleration.

2. If changes in gravitational acceleration result in a disproportionate decrease of the effective mechanical advantage of limbs or reduction in contact time for developing force, then specific resistance may increase.

3. If changes in gravitational acceleration disproportionately increase effective mechanical advantage or the contact time for developing force, then specific resistance may decrease.

4. Finally, changes in the direction and magnitude of gravitational acceleration will affect the energetics and mechanics of animal motility even for small runners that appear to defy gravity.

ACKNOWLEDGEMENTS

I thank Lena Ting for reading the manuscript critically. Research was supported by NSF PYI Award DCB 90-58138. Support for travel was given by Galileo Foundation and USAF Office of Scientific Research.

REFERENCES

- ALEXANDER, R. MCNEILL. Locomotion of animals. Blackie, Glasgow, 1982.
- ALEXANDER, R. McN. AND JAYES, A.S. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool. (London)*. 201: 135-152., 1983.
- BIEWENER, A.A. Design of the mammalian terrestrial locomotor system in relation to body size. *Bioscience*. 39: 776-783, 1989.
- BLICKHAN, R. The spring mass model for running and hopping. *J. Biomech.* 22, 1217-1227, 1989.
- BLICKHAN, R. AND R.J. FULL. Locomotion energetics of the ghost crab: II. Mechanics of the center of mass during walking and running. *J. Exp. Bio.* 130, 155-174, 1987.
- CAVAGNA, G.A., HEGLUND, N.C. & TAYLOR, C.R. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* 233(5), R243-R261, 1977.
- CAVAGNA, G.A., ZAMBONI, A. FARAGGIANA, T., AND MARGARIA R. Jumping on the moon: Power output at different gravity values. *Aerospace Med.* 43, 408-414, 1972.
- FULL, R.J. Locomotion without lungs: energetics and performance of a lungless salamander, *Plethodon jordani*. *Am. J. Physiol.* 251, R775-R780, 1986.
- FULL, R.J. Mechanics and energetics of terrestrial locomotion: From bipeds to polypeds. In: *Energy Transformation in Cells and Animals*, (ed. W. Wieser and E. Gnaiger). Thieme, Stuttgart. pp. 175-182, 1989.
- FULL, R.J. AND TU, M.S. The mechanics of six-legged runners. *J. exp. Biol.* 148, 129-146, 1990.
- FULL, R.J. AND TULLIS, A. The energetics of ascent: insects on inclines. *J. exp. Biol.* 149, 307-317, 1990.
- FULL, R.J., ANDERSON, B.D., FINNERTY, C.M. AND FEDER, M.E. Exercising with and without lungs: I. The effects of metabolic cost, maximal oxygen transport and body size on terrestrial locomotion in salamander species. *J. Exp. Bio.* 138, 471-485, 1988.
- FULL, R.J. ZUCCARELLO, D.A. AND TULLIS, A. Effect of variation in form on the cost of terrestrial locomotion. *J. exp. Biol.* 150, 233-246, 1990.
- GABRIELLE, G. AND VON KARMAN, T. What price speed? *Mech. Eng.* 72, 775-781, 1950.
- HEGLUND, N.C., CAVAGNA, G.A. & TAYLOR, C.R. Energetics and mechanics of terrestrial locomotion. III. Energy changes of the center of mass as a function of speed and body size in birds and mammals. *J. exp. Biol.* 79, 41-56, 1982.
- HEGLUND, N.C. AND TAYLOR, C.R. Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. exp. Biol.* 138, 301-318, 1988.
- HEGLUND, N.C., TAYLOR, C.R. & MCMAHON, T.A. Scaling stride frequency and gait to animal size: mice to horses. *Science*. 186, 1112-1113, 1974.
- HERREID, C.F. & FULL, R.J. Energetics of hermit crabs during locomotion: the cost of carrying a shell. *J. Exp. Bio.* 120, 297-308, 1985.
- JOHN-ALDER, H.B., GARLAND, T. & BENNETT, A.F. Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (*Trachydosaurus rugosus*). *Physiol. Zool.* 59(5), 523-531, 1986.
- KRAM, R. AND R.C. TAYLOR. Energetics of running: a new perspective. *Nature* 346, 265-267, 1990.
- MARGARIA R. AND CAVAGNA, G.A. Human locomotion in subgravity. *Aerospace Med.* 35, 1140-1146, 1964.
- MCMAHON, T.A. AND G.C. CHENG. The mechanics of running does stiffness couple with speed? *J. Biomech.* (in press).
- PACE, N., AND A.H. SMITH. Gravity, and metabolic scale effects in mammals. *Physiologist* 24 Suppl: S37-40, 1981.
- TAYLOR, C.R. Mechanical efficiency: a useful concept? In *Aspects of Animal Movement*. (H.Y. Elder and E.R. Trueman eds.) Cambridge University Press, Cambridge. pp. 235-244, 1980.
- TAYLOR, C.R., S.L. CALDWELL AND V.J. ROWNTREE. Running up and down hills: some consequence of size. *Science*. 178: 1096-1097, 1972.
- TAYLOR, C.R., HEGLUND, N.C. & MALOY, G.M.O. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Bio.* 97: 1-21, 1982.
- TAYLOR, C.R., HEGLUND, N.C., MCMAHON, T.A. & LONNEY, T.R. Energetic cost of generating muscular force during running: a comparison of large and small animals. *J. exp. Biol.* 86, 9-18, 1980.
- TAYLOR, C.R., SCHMIDT-NIELSEN, K., & RAAB, J.L. Scaling of energetic cost to body size in mammals. *Am. J. Physiol.* 210, 1104-1107, 1970.