

# Reports

## Scaling Stride Frequency and Gait to Animal Size: Mice to Horses

**Abstract.** *The stride frequency at which animals of different size change from one gait to another (walk, trot, gallop) changes in a regular manner with body mass. The speed at the transition from trot to gallop can be used as an equivalent speed for comparing animals of different size. This transition point occurs at lower speeds and higher stride frequencies in smaller animals. Plotting stride frequency at the trot-gallop transition point as a function of body mass in logarithmic coordinates yields a straight line.*

The power expended during running varies in a regular manner with body mass, being relatively greater in smaller animals (1). This was predicted by Hill (2), who developed a simple and fairly comprehensive model for scaling running parameters to body size for geometrically similar animals. From his own and others' work on the physiology of muscle, Hill made the reasonable assumptions that two properties of vertebrate muscle are constant over the entire range of body size: (i) the force per cross-sectional area at which maximum power is developed, and (ii) the maximum work per contraction for a given volume of muscle. Hill's model applies only at top speed, which he uses to compare animals of different size. He predicts that at top speed stride length will be proportional to the linear dimensions of the animal or  $(\text{body mass})^{1/3}$  and that stride frequency will be inversely proportional to the linear dimensions of the animal or  $(\text{body mass})^{-1/3}$ . His model also predicts that animals of different size will all be able to reach the same top speed. Since Hill assumes that the maximum work done by a muscle during a stride is proportional to  $(\text{body mass})^{1.0}$ , and that the number of strides per minute at top speed is proportional to  $(\text{body mass})^{-1/3}$ , then the power required for an animal to run at top speed will equal work per stride times strides per minute and thus be proportional to  $(\text{body mass})^{2/3}$ .

There is a fundamental problem with this model: animals are not built in a geometrically similar manner, and the model needs to be refined to take the observed deviations from geometric similarity into account (3). In order

to compare running animals of different size and geometric proportions, one needs to use a comparable speed for the different animals. Hill's choice of top speed is sound, but impractical: How does one know that an animal is running at top speed? If one observes animals of different size running at the

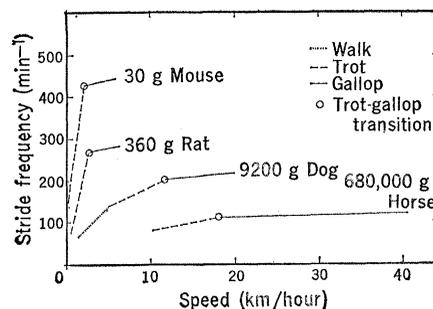


Fig. 1. Stride frequency of mouse, rat, dog, and horse as a function of speed. The relation between speed and stride frequency changes from gait to gait. The trot-gallop transition is marked with a circle.

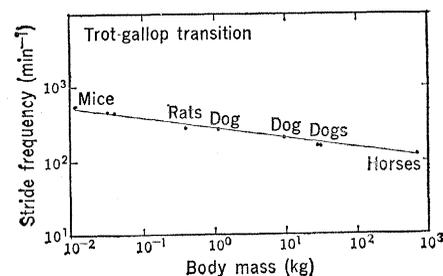


Fig. 2. Stride frequency at the trot-gallop transition point (see Fig. 1) plotted against body mass in logarithmic coordinates. The relation is  $f = 269W^{-0.14}$  where  $f$  is strides per minute and  $W$  is body mass in kilograms. The correlation coefficient for this line calculated by the method of least squares is  $-0.99$ .

same speed, say 6 km/hour, a 500-kg horse is walking slowly, a 10-kg dog is trotting, and a 30-g mouse is galloping. These are clearly not equivalent situations. In order to construct a new scaling model which predicts equivalent stresses and power requirements for running animals of different size, we first required basic information about how stride frequency and gait change as a function of speed.

We measured stride frequency and gait as a function of speed for 4 white mice (9, 20, 29, and 38 g), 3 white rats (average weight 362 g), 3 dogs (1.1, 9.2, and 27.3 kg), and 31 horses (average weight approximately 500 kg). Measurements on the small animals were made while they ran on a treadmill by using a high speed camera (Eclair GV-16 Super, with an optical pulse generator to record elapsed time on the film). The horses were too large to run on our treadmill, so we went to a local racetrack and recorded the stride frequency, gait, and speed of riderless horses while they were being led through their morning exercises.

Stride frequency increased linearly with speed during a walk or a trot, but the slope for each gait was different (Fig. 1). Once an animal started to gallop, frequency remained nearly constant as the animal increased speed: thus all of the increase in speed was the result of increased stride length. The transition from one gait to another occurred at lower speeds and higher frequencies in smaller animals. Since the stride frequency of a galloping animal is nearly constant, the transition from trot to gallop occurs at the maximum sustained stride frequency of an animal. Plotting stride frequency at this transition as a function of body mass in logarithmic coordinates yields a straight line (Fig. 2). Stride frequency, stride length, and running speed at the trot-gallop transition all scale in a regular manner with body mass ( $W$ ) as follows

$$\text{Stride frequency (min}^{-1}\text{)} = 269W^{-0.14};$$

$$r = -0.99$$

$$\text{Stride length (m)} = 0.35W^{0.38}; r = 0.97$$

$$\text{Running speed (km/hour)} = 5.5W^{0.24};$$

$$r = 0.93$$

where  $W$  is in kilograms and  $r$  is the correlation coefficient of a least squares linear regression. We were unable to record the walk-trot transition in smaller animals since we were not able to train them to walk at a constant speed on our treadmills.

Recently, Gold (4) extended Hill's model to cover a range of speeds, arguing that if animals increase speed by increasing stride frequency, and if the work per gram per stride is constant over the entire range of speeds, this would explain the empirical relation between energetic cost of running and body size in mammals (1). We have found that stride frequency and stride length both increase with increasing speed, and that within a gallop speed is increased primarily by increasing stride length while frequency remains nearly constant. At comparable speeds (such as at the trot-gallop transition), however, Gold's argument remains valid for geometrically similar animals. McMahon (3) suggested a model based on elastic similarity whereby animals regularly thicken their proportions as body size increases. Herschman (5) extended Gold's argument to conform to an elastic similarity model and predicted that stride length will be proportional to  $W^{0.375}$ . McMahon (6) has also used his model to predict that running speed is proportional to  $W^{0.25}$  and stride frequency is proportional to  $W^{-0.125}$  at the trot-gallop transition (7). Both Herschman's and McMahon's predictions are in substantive agreement with the data reported here.

We propose that the speed at the trot-gallop transition point is a "physiologically similar speed" for animals of different size. It has the advantage over top speed that it can be easily measured. If one uses this transition point to construct new scaling models, however, it is important to understand why animals change gait at this point. It seems likely that at the transition to each gait additional elements of the body are recruited for storage of elastic energy, with little energy being stored in elastic elements during walking, energy being stored in the elastic elements of the limbs during trotting, and finally, the entire trunk being involved in elastic storage during galloping. This remains very speculative and much more work is needed before the reasons for changing gaits can be clearly defined.

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3. T. A. McMahon, *Science* **179**, 1201 (1973).
4. A. Gold, *ibid.* **181**, 275 (1973).
5. A. Herschman, *Am. J. Phys.* **42**, 778 (1974).
6. T. A. McMahon, in preparation.
7. As explained in (3), elastic similarity between animals of different body weight requires that the diameter ( $d$ ) of every element (bone, muscle, limb) be maintained proportional to the  $3/2$  power of the length ( $l$ ) of that element. Thus  $l$  increases as  $W^{1/3}$ , but  $d$  increases as  $W^{3/8}$ . Suppose a stimulated muscle and its tendon are thought of as a spring, and this

spring acts at each joint as a restoring force against forces produced by inertia. For a sufficiently large number of joints, we can model the skeleton and its musculature as a continuous beam, for which the group  $f^{2H}/d^2$ , where  $f$  is the natural frequency, is a constant (eigenvalue) in a given mode of vibration. Setting  $l \propto W^{1/3}$  and  $d \propto W^{3/8}$ ,  $f$  is proportional to  $W^{-1/8}$ . Galloping animals are thus seen as mass-spring-lever systems vibrating at their resonant frequencies. By fixing their stride length at the trot-gallop transition proportional to  $d$  and hence proportional to  $W^{3/8}$ , they fix their speed proportional to  $fd$  or  $W^{-1/8+3/8} = W^{1/4}$ .

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## Vermetid Gastropods and Intertidal Reefs in Israel and Bermuda

**Abstract.** *Small-rimmed intertidal reefs develop in the subtropical marine waters of Israel and Bermuda when erosion of exposed promontories is arrested by vermetid gastropods. The reefs in Bermuda are actively growing, wave-resistant biogenic structures, while those in Israel are limestone structures only encrusted by a relatively thin layer of vermetid shells cemented by coralline algae.*

Several species of vermetid gastropods are gregarious, and encrust intertidal bench-like ledges or form massive reefs (1). This report describes reefs in Shikmona, on the Mediterranean coast of Israel (32°49'N, 34°57'E), and in Bermuda, which is at the same latitude and has several similar physical marine conditions (2). In both cases vermetids have a significant role in reef development (3). The reefs are small intertidal formations 2 to 5 m in diameter resembling miniature atolls (Fig. 1) and are usually circular with raised, overhanging rims somewhat higher at the seaward side. They enclose a shallow basin with a flat bottom in Shikmona and a deep cup-shaped hollow in Bermuda.

The Shikmona reefs are made of limestone encrusted by vermetids. The limestone relief is leveled off and surrounded by an elevated rim about 10 cm high, covered by a crust of *Dendropoma petraeum* (Monterosato) 10 to 15 cm thick. The basin is covered by a crust of *Vermetus triquetrus* Bivona-Bernardi 2 to 4 cm thick. The rim is incessantly swept by the surf and is exposed to the air at low tide; the basin is protected from the full impact of the waves and from exposure to air by the water retained by the rim. Correspondingly, the short, rugged shell of *D. petraeum* is tightly sealed, with a wide operculum which protects the animal from predators, desiccation (4), and wave impact. The shell of *V. triquetrus* is longer and thinner, with a fragile, upturned terminal part, and the tiny operculum is nonfunctional, allowing the animal to withdraw deep into the shell (4).

Both species are plankton-feeders. *Vermetus* produces a mucus web, and agitation at the reef's rim would probably render its employment difficult. *Dendropoma petraeum* filter-feeds through a well-developed gill (5), and turbulence at the reef's rim ensures a food supply and facilitates water inhalation.

In Shikmona "microatolls" form on rocky promontories that have been chemically and biologically (6) eroded into basin-shaped depressions surrounded by slightly elevated rims. When erosion lowers the basin to fall within the narrow vertical range of the vermetids, the water-covered surface becomes colonized by *V. triquetrus*. The top of the seaward edge, which is exposed to the waves, becomes encrusted by *D. petraeum*. This cemented crust apparently stabilizes the substrate against further erosion. A small-rimmed ledge is thus established at the seaward side of the promontory. It is then progressively widened when solution basins located farther leeward are eroded to the level where *V. triquetrus* can flourish. The direction of the incident waves varies with the configuration of the shore. Reflected backwash from other rocky promontories initiates at the lee side the same processes that have previously taken place at the seaward side, until the promontory becomes surrounded by a rimmed edge from all sides. Eventually, when all rock remnants have been eroded to the level of effective vermetid growth, a miniature atoll is formed, whose rim and enclosed basin are preserved by the protective growth of *Dendropoma* and *Vermetus*, respectively (Fig 1). The upward growth of