How fast do living organisms move: Maximum speeds from bacteria to elephants and whales

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Despite their variety and complexity, living organisms obey simple scaling laws due to the universality of the laws of physics. In the present paper, we study the scaling between maximum speed and size, from bacteria to the largest mammals. While the preferred speed has been widely studied in the framework of Newtonian mechanics, the maximum speed has rarely attracted the interest of physicists, despite its remarkable scaling property; it is roughly proportional to length throughout nearly the whole range of running and swimming organisms. We propose a simple order-of-magnitude interpretation of this ubiquitous relationship, based on physical properties shared by life forms of very different body structure and varying by more than 20 orders of magnitude in body mass. © *2015 American Association of Physics Teachers.*
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I. INTRODUCTION

A fundamental property of many living organisms is autonomous locomotion. On Earth, which is a rocky planet of surface temperature $T \simeq 300\,K$ with liquid water and an atmosphere, animals can run, swim, and/or fly. Each individual has a preferred speed of locomotion which is determined by its size and by dynamical constraints,[1,2] depending on the means of locomotion and the ambient conditions. Newtonian mechanics tells us that a walker of size L approximated as an inverted pendulum in the Earth's gravitational field g, moves at angular frequency $(g/L)^{1/2}$; hence its preferred speed V is of order of magnitude the step length $\sim L$ times the frequency: $V \sim (Lg)^{1/2}/2\pi$. More elaborate arguments have been used to propose scalings for various means of locomotion, depending on such factors as the gravity and the density of the surrounding medium.[3–7]

However, when living organisms are driven by circumstances to move as fast as possible, they may increase their speed above the preferred speed. As human beings, we can increase our speed by one order of magnitude by running. The fastest human sprint speed on record is 12.2 m/s for Usain Bolt (size $L = 1.96$ m and mass $M = 86$ kg in 2009),[8] whereas the recent 50 m swimming record of Florent Manaudou ($L = 1.99$ m, $M = 99$ kg) corresponds to an average speed of 2.5 m/s. For comparing organisms of widely different sizes, it is more appropriate to express the speed in terms of the body length. The above values yield 6.1 and 1.2 lengths per second, respectively. Near the lower extreme of the size range, the 2.5-μm-long bacterium *Bacillus subtilis* can swim at 15 μm/s, or 6 lengths/s, strikingly close to Usain Bolt's running performance. A 4-mm-long ant runs at 60 mm/s (15 lengths/s), whereas a 2.1-m ostrich runs at 23 m/s (11 lengths/s).[4] These examples reflect a ubiquitous property of living organisms: the maximum speed of running and swimming lies between 1 and 100 lengths per second, in an overall mass range covering nearly 20 orders of magnitude, as first noted by Bonner in a classic book.[9]

Indeed, while maximum speeds V_{max} and lengths L vary by nearly 7 orders of magnitude (and mass by three times more), maximum relative speeds V_{max}/L remain constant at

ten per second with an accuracy of a factor of ten,[4,9–11] even though different scalings hold over narrower mass ranges.[12,13] This large-scale pattern, which holds for organisms as diverse in overall structure, means of locomotion, and surrounding medium as eight-legged mites and two-legged ostriches, from small bacteria to large mammals, has apparently not been appreciated by the physics community and requires a basic explanation. A solution was proposed by Dusenbery,[11] but being based on viscous drag it only applies to the small range of organisms swimming at low Reynolds numbers.

In the present paper, we illustrate the approximate linear relation between maximum speed and body size for a large number of running and swimming species from micro-organisms to the largest mammals (Sec. II), and we propose a simple order-of-magnitude interpretation, based on three basic properties of living beings that constrain their performances: their density ρ, the applied force per unit cross-sectional area σ, and the maximum rate of energy consumption per unit mass b_M. These three quantities are known to be roughly independent on size over virtually the full mass range of moving species, as summarized in Sec. III. We shall briefly discuss in Sec. IV two exceptions to the large-scale relation $V_{max}/L \sim 10$ s^{-1}: very large organisms, whose maximum speed tends to level off,[4,12] and flyers.

The huge mass range studied enables us to estimate orders of magnitude by neglecting specific details that are important in scaling studies over narrower mass ranges. In this sense, the present paper can be viewed as an exercise at the boundary between comparative zoology and order-of-magnitude physics inspired by Victor Weisskopf's physics courses.[14,15] As usual, the symbol $\sim$ means that two quantities are equal to within one order of magnitude or so, whereas $\simeq$ means equal within a factor of two or so. Unless otherwise stated, units are SI.

II. EMPIRICAL RESULTS

Figure 1 shows the measured maximum relative speed V_{max}/L as a function of mass for running and swimming, from micro-organisms to the largest mammals. The mass
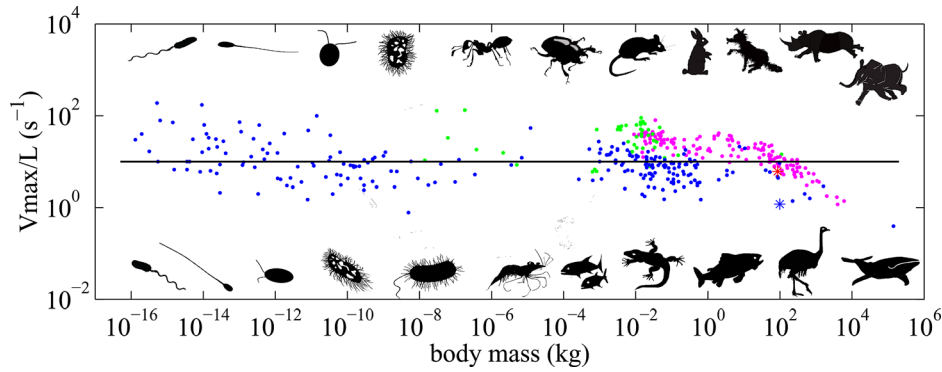
Fig. 1. Maximum relative speed versus body mass for 202 running species (157 mammals plotted in magenta and 45 non-mammals plotted in green), 127 swimming species and 91 micro-organisms (plotted in blue). The sources of the data are given in Ref. 16. The solid line is the maximum relative speed [Eq. (13)] estimated in Sec. III. The human world records are plotted as asterisks (upper for running and lower for swimming). Some examples of organisms of various masses are sketched in black (drawings by François Meyer).

range goes from mites to the African bush elephant for running and from micrometer-sized bacteria to whales for swimming. Almost all the data lie in the range $1 < V_{max}/L < 100$. This range is remarkably narrow compared to the 10^{20}-fold variation in body mass and confirms the striking constancy of the maximum relative speed first noted by Bonner.[9] The human world records for running and swimming are plotted as asterisks (red and blue, respectively). Both lie in the lower range of animal running and swimming relative speeds, respectively, illustrating the low rank of human beings in the animal world for sprinting and swimming. Nevertheless, these records still lie within an order of magnitude of the scaling $V_{max}/L = 10\ \mathrm{s}^{-1}$.

Figure 1 also suggests that the maximum speed tends to level-off for large masses,[4] a question that we shall discuss in Sec. IV. We have not plotted flying speeds, which follow a different scaling law (see Sec. IV).[4]

III. ESTIMATION OF MAXIMUM SPEED

In order to propose a basic interpretation of the observed scaling, let us consider the three universal properties of living species which constrain their maximum speed of locomotion: mass density ρ, applied force per unit cross-sectional area σ, and maximum power per unit mass b_M (maximum metabolic rate).

A. Three ubiquitous properties of living species

First, the mass density of organisms is roughly that of liquid water, on which life on Earth is based

$$\rho \simeq 10^3\ \mathrm{kg\,m^{-3}}. \tag{1}$$

Second, the applied force per unit cross-sectional area of tissue[6,17] is of order of magnitude

$$\sigma \sim 2 \times 10^5\ \mathrm{Nm^{-2}}, \tag{2}$$

from micro-organisms to the largest animals.[18] This is an example of the rule dating back to Galileo that the strength of an object is proportional to its cross-section. Here, Eq. (2) is not the resistance to fracture, the so-called tensile strength, but the average active tension applied by organisms for their locomotion. This tension has a similar value for all organisms because it is based on biological molecular motors of

similar basic properties. Biological motors are molecules converting chemical energy into mechanical energy via a conformational change in their molecular structure.[19] This 3-dimensional structure is held together by non-covalent bonds, with the typical free energy

$$W_0 \sim 10\ k_B T, \tag{3}$$

which prevents their destruction by thermal agitation, and their typical size is[20]

$$a_0 \sim e^2/4\pi\epsilon_0 W_0 \sim 6\ \mathrm{nm}, \tag{4}$$

despite the complexity of electrostatic interactions within large molecules.[21] Basically, a molecular motor uses an energy $\sim W_0$ for moving by one "step" via a change in 3-D structure, so that the "step" length is $\sim a_0$. The elementary force is thus

$$F_0 \sim W_0/a_0 \sim 7\ \mathrm{pN} \tag{5}$$

over an equivalent cross-section area whose order of magnitude is a_0^2, so that the force per unit cross-section area is

$$\sigma \sim F_0/a_0^2 \sim W_0/a_0^3. \tag{6}$$

Substituting Eqs. (3) and (4) into Eq. (6) yields Eq. (2).

This order of magnitude holds for muscles of animals, which are made of filaments containing hundreds of elementary motors (myosin), as well as for the moving appendages of micro-organisms.[18,22,23]

Third, consider the power available. Transport of heat and nutrients takes place across surfaces, which are expected to scale as the square of size, and thus to vary with body mass as $M^{2/3}$; therefore, the energy consumption rate of living beings (the so-called "metabolic rate") per unit mass is expected to scale as $M^{2/3}/M = M^{-1/3}$. Reality is more complicated because body shape and structure change with size, so that different scalings are observed[24] with an exponent closer to $-1/4$ than to $-1/3$. After decades-long controversies,[25,26] it has been shown, albeit rarely appreciated in the physics community, that the basal metabolic rate per unit mass remains roughly constant across life forms.[27,28] More precisely, for the vast majority of organisms it remains within a 30-fold range,[29] which is remarkably narrow compared with the $\sim 10^{20}$-fold body mass range concerned. Since

we wish to estimate the maximum speed, the relevant property is not the basal metabolic rate but rather the maximum metabolic rate. The order of magnitude of this parameter has been shown to be roughly constant, too, when scaled to the mass, with the value

$$b_M \sim 2 \times 10^3 \ \mathrm{W\,kg^{-1}} \tag{7}$$

per unit of working tissue.[27,30,31]

B. Maximum relative speed

If the maximum relative speed V_{max}/L only depends on the parameters ρ, σ, and b_M, dimensional analysis can be used to deduce its scaling. In terms of the three dimensions $[M]$, $[L]$, $[T]$, the density scales as

$$\rho \propto [M][L]^{-3}. \tag{8}$$

Since σ is a force ($\propto [M][L][T]^{-2}$) per unit cross-section ($\propto [L]^2$), it scales as

$$\sigma \propto [M][L]^{-1}[T]^{-2}, \tag{9}$$

and since b_M is a power ($\propto [M][L]^2[T]^{-3}$) per unit mass, it scales as

$$b_M \propto [L]^2[T]^{-3}. \tag{10}$$

Therefore, since $V_{max}/L \propto [T]^{-1}$, we deduce

$$V_{max}/L \propto b_M \rho/\sigma. \tag{11}$$

In order to make a quantitative estimate, let us go a step further than dimensional analysis. First, consider running and swimming of animals beyond the micro-organism range. At zero order, both means of locomotion can be considered as a cyclic process (of frequency f) in which an organism of length L moves by one "step" of length $\sim L$ during each cycle, by contracting muscles. Consider an organism of cross-section S and length L:

- its mass is $M \sim \rho S L$,
- moving by one step of length $\sim L$ by applying the force $\sim \sigma S$ requires the energy per unit mass $w \sim \sigma S L/M \sim \sigma/\rho$,
- since f steps per second consume the energy fw per unit mass, which must be smaller than b_M, the maximum step rate is $f_{max} \sim b_M/w \sim b_M \rho/\sigma$.

The maximum speed equals the step length $\sim L$ times the maximum step rate f_{max}, whence

$$V_{max}/L \sim f_{max} \sim b_M \rho/\sigma. \tag{12}$$

Substituting Eqs. (1), (2), and (7) into Eq. (12) yields

$$V_{max}/L \sim 10 \ \mathrm{s^{-1}}, \tag{13}$$

which is the large-scale relation mentioned in the Introduction.

Consider now micro-organisms. They move by rotating or undulating flagella, cilia, or pili, which are operated by molecular motors as are the muscles of larger organisms, even though the number of motors is much smaller for micro-organisms. In this case, it is more enlightening to consider

the microscopic level. During one period of rotation or undulation,[23,32] a micro-organism of length L moves along a distance $\sim L$ using energy $\sim W_0$ [given in Eq. (3)] per molecular motor. With f cycles per second, the power spent is $\sim f W_0$. For a motor of size $\sim a_0$ given in Eq. (4) and mass $\sim \rho a_0^3$, the power cannot exceed the maximum metabolic rate $\sim b_M \rho a_0^3$. This yields $f \lesssim b_M \rho a_0^3/W_0$, whence

$$V_{max}/L \sim b_M \rho a_0^3/W_0. \tag{14}$$

With n motors, both the numerator and the denominator of Eq. (14) are multiplied by n, which does not change the result. Since from Eq. (6) $\sigma \sim W_0/a_0^3$, Eq. (14) is equivalent to Eq. (12).

Hence, both micro-organisms and larger animals should have a similar maximum relative speed for running and swimming, given by Eqs. (12)–(13), in agreement with the data plotted in Fig. 1.

IV. CONCLUDING REMARKS

There are two exceptions to the scaling derived above: flying species and very large organisms.

Flying is outside the scope of our simplified model because in that case the muscles essentially govern wing flapping, and this frequency does not yield the total relative speed of the organism. In addition, air drag represents the dominant constraint at large flying speeds.[4]

Consider now large running and swimming organisms, for which V_{max}/L tends to decrease (Fig. 1), even though the data do not lie below one order of magnitude of the scaling (13) except for the largest animal. Several effects become important at high speeds, such as friction and excess heat production. However, Fig. 1 suggests a similar trend for running and swimming, which points to a more fundamental limitation, independent of the surrounding medium.

Let us consider an organism of cross-section S and length L, as in Sec. III B, and approximate the locomotion as a periodic motion of legs (for running) or tail (for swimming) of length $\sim L$. The maximum frequency is constrained not only by the power available, as considered in Sec. III B, but also by the maximum angular acceleration that muscles can provide. With the torque $\Gamma \lesssim \sigma S L$ and moment of inertia $I \sim M L^2 \sim \rho S L^3$, the angular acceleration $d^2\theta/dt^2 \sim \Gamma/I$ is constrained by

$$d^2\theta/dt^2 \lesssim \sigma/(\rho L^2). \tag{15}$$

Integrating Eq. (15) twice yields the order of magnitude of the time for the appendage to be accelerated up to a fixed angle θ:

$$t \gtrsim L(\rho\theta/\sigma)^{1/2}. \tag{16}$$

Setting $\theta \sim 1$ in Eq. (16) yields the frequency $f \sim 1/t \lesssim (\sigma/\rho)^{1/2}/L$ and therefore the upper limit of the maximum speed

$$V_{max} \lesssim (\sigma/\rho)^{1/2}. \tag{17}$$

Hence, the value of V_{max}/L in Eq. (12) can only hold for

$$L \lesssim (\sigma/\rho)^{1/2}/(b_M \rho/\sigma) = (\sigma/\rho)^{3/2}/b_M. \tag{18}$$

Substituting Eqs. (1), (2), and (7) into Eq. (18) yields $L \lesssim 1.4$ m. This limitation prevents larger organisms from following Eq. (12), which suggests that the maximum speed should increase linearly with body length only up to (approximately) meter-sized organisms, in agreement with Fig. 1. Consider the blue whale (blue point at $M \simeq 1.5 \times 10^5$ kg), which lies below one order of magnitude of the scaling (12)–(13); with its length $L \simeq 26$ m, Eq. (17) yields $V_{max}/L \lesssim 0.5$ s^{-1}, a limit close to the observed value plotted in Fig. 1.

Finally, one should be reminded that in the spirit of this paper, Eqs. (12) and (17) are order-of-magnitude results. Because of the huge diversity of organisms and sizes, we have ignored the specific methods of locomotion, using drastic approximations for the applied forces, cross-sections and distances involved, as well as approximating by unity the efficiency of energy conversion and the proportion of active tissue. The numerous correction factors tend to cancel out in the final order-of-magnitude result.

In conclusion, we explain the ubiquity of the maximum relative speed at about ten lengths per second for running or swimming, from bacteria to large mammals, by the ubiquity of the density, the applied force (per unit cross-sectional area), and the maximum metabolic rate (per mass of active tissue). The maximum absolute speed is limited by the maximum acceleration that muscles can provide, which may explain why animals larger than the ostrich do not move faster.

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