OPERATION OF THE SYSTEM FOR DEVELOPMENT OF FORCE, SPEED AND POWER

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THE MAXIMUM FORCES EXERTED BY ANIMALS

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SUMMARY

This paper reviews the maximum forces exerted by animals in a wide range of activities including running, jumping, swimming and biting. Most of the data refer to vertebrates and arthropods, ranging in size from 0·5-mg fleas to 3-tonne elephants. Maximum forces exerted on the environment give values of (force/body weight) which lie, in most cases, between 0·5 body mass$^{-1/3}$ (kg) and 20 body mass$^{-1/3}$. Maximum forces exerted by major muscle groups give values of (force/body weight) in most cases between 10 body mass$^{-1/3}$ and 50 body mass$^{-1/3}$.

INTRODUCTION

This paper is about the maximum forces exerted by animals, in a wide range of activities. The forces in the muscles themselves, as well as the forces exerted on the environment, are discussed.

Such discussions must take account of the sizes of the animals. In general, large animals exert larger forces than small ones, but these forces cannot be expected to be proportional to body mass. Consider two geometrically-similar animals of different sizes, with corresponding parts of their bodies made of materials of equal strength and density. The forces they can exert will be proportional to the cross-sectional areas of their parts, and therefore to the squares of their linear dimensions. Their masses will be proportional to their volumes and therefore to the cubes of their linear dimensions. The maximum forces should thus be proportional to body mass$^{2/3}$. Real animals of different sizes are not, in general, geometrically similar, and the relationship between maximum force and body mass will be investigated.

Most of the information that will be presented refers to vertebrates and arthropods. Relatively little is known about the forces exerted by other groups of animals.

DATA

The data have been collected from many sources.

Running

The faster an animal runs, the smaller in general is the fraction of the stride for which each foot is on the ground. The feet must therefore exert larger forces, while on the ground, to make the average force over the complete stride match body weight.

Key words: Force, muscle, locomotion.

Consider an animal of mass m, weight mg, running with duty factor β. (The duty factor is the fraction of the duration of the stride for which each foot is on the ground.) If this animal is a biped, the peak force on a foot can be estimated as $\pi mg/4\beta$ (Alexander, Maloiy, Njau & Jayes, 1979*b*). If it is a typical quadrupedal mammal, supporting 60% of its weight on its fore feet, the peak forces can be estimated as $0{\cdot}15\,\pi mg/\beta$ (for fore feet) and $0{\cdot}10\,\pi mg/\beta$ (for hind feet). The feet are generally not set down simultaneously, so the forces on them cannot meaningfully be totalled. The data that will be presented for running are the largest force exerted by any one foot.

Alexander, Langman & Jayes (1977) filmed antelopes and other ungulates in their natural habitat in Kenya, making them run as fast as possible by pursuing them with a vehicle. The minimum duty factors shown in their films have been used to calculate maximum forces. Similar data are available for buffalo (*Syncerus*) and elephant (*Loxodonta*) (Alexander *et al.* 1979*a*); rhinoceros (*Diceros*, Alexander & Jayes, 1983); camel (*Camelus*, Alexander *et al.* 1982); greyhound (*Canis*, Jayes & Alexander, 1982); rabbit (*Oryctolagus*) and squirrel (*Sciurus*) (Dimery, 1984); hare (*Lepus*) and cheetah (*Acinonyx*) (Hildebrand, 1977) and ostrich (*Struthio*, Alexander *et al.* 1979*b*). Maximum forces on hind feet, calculated from these data, range from 4·3 times body weight for a hare (estimated mass 2·4 kg) to 1·0 times body weight for an elephant (2500 kg).

In other investigations, force platforms have been used for direct measurement of forces exerted in running. Maximum speeds could not generally be obtained because the observations had to be made in laboratories, but data will be presented for humans (Alexander & Vernon, 1975*b*), kangaroos (*Macropus*, Alexander & Vernon, 1975*a*) and small rodents (Biewener, 1983).

In several of the investigations listed in this subsection, forces in muscles have been calculated, as well as forces on the ground. The muscle forces that will be presented are the total force exerted by one major group of muscles, such as the quadriceps femoris or triceps surae of one leg.

Jumping

Small insects accelerate over very short distances when they jump, achieving spectacularly high accelerations. Accelerations measured from films have been used to calculate the forces exerted on the ground by jumping insects, ranging from 0·5-mg fleas (*Spilopsyllus*) to 3-g locusts (*Schistocerca*) (Bennet-Clark & Lucey, 1967; Ker, 1977; Evans, 1973; Bennet-Clark, 1975). A 40-mg click beetle (*Athous*) exerts 380 times its weight, but exerts it with its back, not its legs; it jumps from a lying position by bending its back suddenly (Evans, 1973).

Accelerations calculated from films of frogs jumping indicate forces of about three times body weight, for frogs of masses of 1–30 g (*Pseudacris* and *Rana*, Emerson, 1978). A 250-g bushbaby (*Galago*) made a remarkable jump to a height of 2·3 m, which seems to have required a force of 18 times body weight (Hall-Craggs, 1965). Force platform records of a dog (*Canis*) jumping showed a peak force of 3·2 times body weight, exerted while both hind feet were on the platform (Alexander, 1974).

In most cases, jumping involves two legs exerting peak forces simultaneously. In the peculiar case of the click beetle, the legs are not involved. The forces that will be presented for jumping are total forces on the ground, irrespective of the number of legs involved. This should be remembered when comparisons are made with the data for running, which refer to individual feet. The muscle forces that will be presented refer to the muscles of one joint.

Pushing and pulling

Evans (1977) used a miniature force platform to measure the forces exerted by the hind legs of beetles, as they forced their way under a heavy hinged flap. He obtained data for beetles of masses 16–350 mg, and calculated the force exerted by a major leg muscle in the largest beetle. Taylor (1957) found that sledge dogs exert traction forces up to 0·38 times body weight. Björck (1958) reported draught horses exerting pulls up to 0·41 times their weights.

Swimming

Webb (1978) collected data on the accelerations of fishes. The highest accelerations indicated forces of 4–5·3 times body weight (calculated from Newton's second law of motion, ignoring the added mass of water accelerated with the fish). Alexander (1980) calculated that the muscles of one side of the body of an accelerating trout (*Salmo*) exerted a force of 54 times body weight.

Trueman and his collaborators tethered cephalopods to a force transducer and recorded the forces they exerted, as they tried to swim away by jet propulsion (Trueman, 1980). These were all less than 1·5 times body weight.

Flight

Flight requires a mean lift force equal to body weight, but if lift fluctuates during a wingbeat cycle, the peak lift must be larger. A film of a Kori bustard (*Ardeotis kori*) taking off shows (by the bending of the feathers) that the lift is generated during the downstroke, which occupies 0·6 of the duration of the wingbeat cycle. Peak lift must therefore be at least 1/0·6 = 1·7 times body weight. This seems to be the heaviest flying bird, attaining masses up to at least 16 kg (personal observation). Smaller flying animals seem to fly more easily, and no data for them are presented.

Nipping

Brown, Cassuto & Loos (1979) measured the forces required to pull open the chelae of decapod crustaceans. Some of these forces were very high, notably 310 times body weight for a 1·9-g crab. The forces that will be presented are the largest recorded, and were applied near the base of the claw. Brown *et al.* (1979) also give the (smaller) forces that were required when applied near the tip of the claw, and the mechanical advantages of the muscles for forces applied at the tip. Thus it has been possible to calculate the forces exerted by the closer muscles.

Biting

Bite forces have been recorded by inducing animals to bite force transducers. This has been done for humans (Linderholm & Wennström, 1970), two other primate species (Hylander, 1979) and various reptiles (Sinclair, 1983). Hylander did not give the masses of his specimens but it will be assumed that they were typical for their species (1·1 kg for *Galago crassicaudatus* and 5 kg for *Macaca fascicularis*). The data that will be presented are the largest recorded forces, from any part of the mouth.

DISCUSSION

The data for external forces are shown in Fig. 1 and those for muscle forces in Fig. 2. In each case (force/body weight) is plotted against body mass. This makes the graphs more compact than they would be, if force itself had been plotted.

As shown in the Introduction, geometrically similar animals of different sizes could be expected to exert forces proportional to body mass$^{2/3}$, with corresponding parts of their bodies. Thus (force/weight) should be proportional to body mass$^{-1/3}$. However, even quite closely related animals may be far from geometrically similar, and may exert forces with different parts of their bodies. It is not really surprising to find that a 40-mg click beetle exerts 0·15 N with its back, when it jumps, while a 38-mg carabid beetle exerts only 0·01 N with its legs, when it pushes (Evans, 1973, 1977). Similarly, it is not very surprising that a 137-g crab can nip with a force of 36 N, although a 130-g jellyfish (*Carybdea*) can exert only 0·02 N by its swimming movements (Brown *et al.* 1979; Trueman, 1980).

Though animals of equal mass may exert very different maximum forces, most of the points in Fig. 1 lie between the two lines, which show (force/weight) equal to 0·5 body mass$^{-1/3}$ and 20 body mass$^{-1/3}$ (body mass in kg). The position of the lower line depends on the rather arbitrary decision that some activities are not sufficiently forceful to merit inclusion on the graph. If less forceful activities had been included, the line would have had to be placed lower.

The legs of insects are operated by muscles with low mechanical advantages, and forces exerted by insect legs all lie near the lower of the two lines in Fig. 1. These are forces exerted by beetles pushing, and by other insects jumping. In contrast, the jaws of mammals and reptiles and the chelae of crabs are operated by muscles with high mechanical advantages, and the points for biting and nipping lie nearer the upper line. Points for forces exerted by the feet of large mammals also lie near the upper line.

There seems to be some tendency for points for large animals to lie near the upper line, and for points for small ones to lie near the lower one. This may be an artefact of the selection of data. Alternatively, it may perhaps indicate a tendency for maximum forces to be proportional to body mass to a power greater than 2/3. Alexander, Jayes, Maloiy & Wathuta (1981) investigated the allometry of mammal leg muscles and suggested that mammals of different sizes should be able to exert forces proportional to body mass$^{0·9}$. This was because large mammals have stronger leg muscles than geometric similarity with small mammals would require, and because the mechanical advantages of the muscles are larger than in small mammals.

Muscle forces are shown in Fig. 2. There are fewer data than in Fig. 1, so it is harder to draw clear conclusions, but the data seem to occupy a narrower band. The

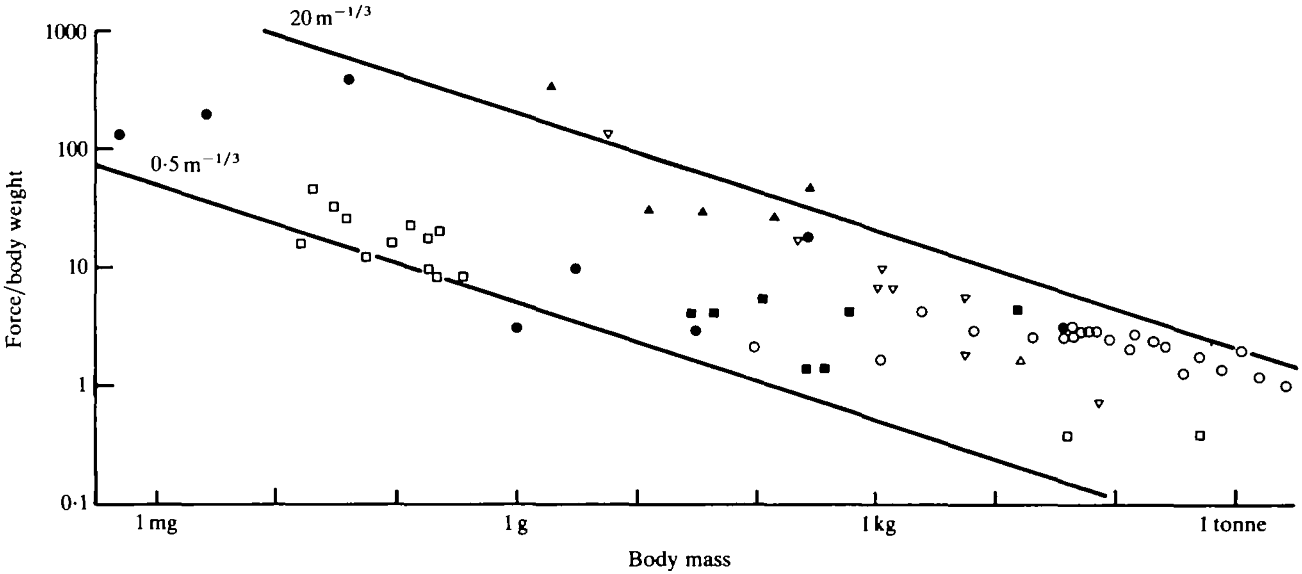

Fig. 1. A graph showing maximum forces exerted by animals on the environment, in various activities. (Force/body weight) is plotted against body mass, on logarithmic coordinates. The points refer to ○, running; ●, jumping; □, pushing and pulling; ■, swimming; △, flight; ▲, nipping; ▽, biting. The lines are (force/weight) = 0·5 body mass$^{-1/3}$ (kg) and (force/weight) = 20 body.mass$^{-1/3}$ (kg).

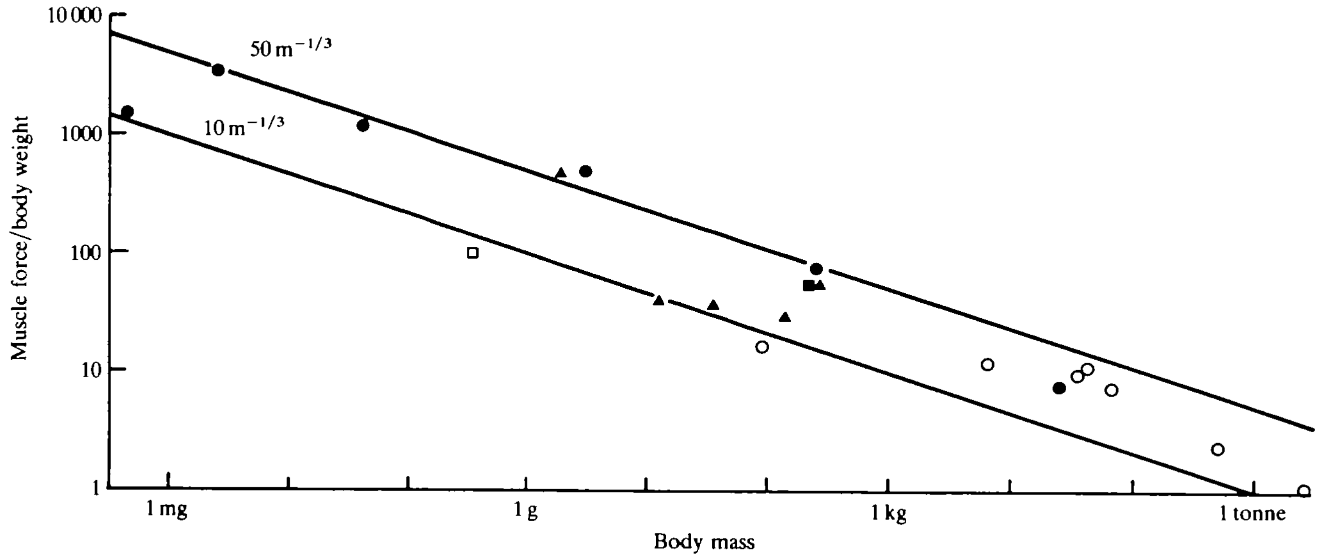

Fig. 2. A graph showing maximum forces exerted by major muscles or groups of muscles, in various animals and activities. Other details as in Fig. 1, except that the lines are (force/weight) = 10 body mass$^{-1/3}$ (kg) and (force/weight) = 50 body mass$^{-1/3}$ (kg).

two lines are separated by a factor of only 5, whereas the lines in Fig. 1 are separated by a factor of 40.

The forces, that muscles of given dimensions can exert, depend on the stresses they can develop. Vertebrate striated muscles can exert isometric stresses of about 0·3 MPa (Close, 1972). Stresses close to this are known to be developed in major leg muscles of various mammals, in fast running and jumping (see Alexander *et al.* 1979*a*; Jayes & Alexander, 1982). Insect muscles with myofilaments of different lengths develop isometric stresses between about 0·3 and 0·7 MPa (Bennet-Clark, 1975). Muscles with longer myofilaments develop larger stresses. The stresses developed by the principal muscles involved in jumping have been calculated to be about 0·3 MPa in a flea and a click beetle (Bennet-Clark & Lucey, 1967; Evans, 1973) and 0·7 MPa in a locust (which has long myofilaments in these muscles, Bennet-Clark, 1975). A major leg muscle of the beetle *Carabus* exerts 0·2 MPa in pushing (Evans, 1977). Thus many of the muscle forces recorded in Fig. 2 involve near-maximal stresses in the muscles concerned. However, other groups of animals have evolved muscles capable of exerting higher isometric stresses, up to 1·4 MPa in some mollusc muscles (Ruegg, 1968). Such muscles are very slow, which may be why they do not occur more widely.

Even if the isometric stress is fixed, the force that can be developed by a muscle of given size and shape can be varied, by varying the pattern of pennation. A pennate muscle composed of a large number of short fibres can exert more force than if it were composed of a smaller number of longer fibres. It has already been noted that large mammals tend to have stronger leg muscles than if they were geometrically similar to small mammals. This is partly because their proximal leg muscles are disproportionately large and partly because their pennate distal leg muscles have disproportionately short muscle fibres (Alexander *et al.* 1981).

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