

Living in a physical world III. Getting up to speed

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1. Introduction

Generalizations in biology come hard, so we treasure any that cut through life's overwhelming diversity. In his famous essay, "On Being the Right Size," J B S Haldane (1926) notes that jumping animals of whatever size should reach the same maximum height; Haldane attributes the insight to Galileo. Other iconic figures make the same assertion—Giovanni Alphonso Borelli (1680), grandfather of biomechanics; D'Arcy Thompson (1942), godfather of biomechanics; and then A V Hill (1938), father-figure for muscle physiologists.

The basic reasoning is straightforward. The force of a muscle varies with its cross-sectional area. The distance a muscle can shorten varies with its length. So the work a muscle can do will vary with the product of the two, in effect with its mass. All mammals have about the same mass of muscle relative to mass, about 45%, and other jumping animals differ only a little more. Thus the work available for a jump should be proportional to body mass. At the same time, the energy, mgh , required to achieve a given height, h , should also be proportional to body mass, m (gravitational acceleration, g , of course, stays constant).

Put in slightly different terms, launch speed, v_0 , sets height for a projectile shot upward, and kinetic energy at launch is $\frac{1}{2}mv_0^2$. So the energy required to achieve a given launch velocity, like the work available, will be proportional to body mass. Either way, height should not depend on body mass.

As Borelli (1680), in the first great treatise on biomechanics, put it "...if the weight and mass of a dog is a fiftieth of those of a horse [] the motive force of the dog would be a fiftieth of that of the horse. Therefore, if the other conditions are equal [], the dog will jump as far as the horse." ('Force' for Borelli meant something close to what we recognize as work or energy.)

The last essay (Vogel 2005) focused on the behaviour of ballistic projectiles after launch. This one fleshes out the story by looking at what happens prior to launch, how projectiles of diverse sizes and functions reach their similar launch speeds.

2. The scaling of acceleration

What does constant jump height imply about prelaunch acceleration? The smaller the creature, the shorter the distance over which it can accelerate to that standard launch speed and the higher its acceleration. That, though, raises no apparent problem for muscle-driven launches. If force, F , scales with length squared (muscle cross section) and mass scales with length cubed (muscle volume), then by Newton's second law, $a = F/m$, acceleration, a , should scale inversely with body length: $a \propto l^{-1}$ —small jumpers should naturally achieve higher accelerations. Consider two adept mammalian jumpers. A lesser galago (or bushbaby) with a leg extension of about 0.16 m accelerates at 140 m s^{-2} while an antelope with a leg extension of 1.5 m accelerates at only 16 m s^{-2} (Bennet-Clark 1977). The comparison comes close to the predicted inverse proportionality—so far, so good.

How does acceleration scale when we look beyond such muscle-powered animal systems and include other projectiles such as those whose trajectories were examined in the previous essay? Table 1 compares body (or projectile, for non-jumpers) size with data or estimates for prelaunch acceleration. Bear in mind its limitations. (i) Its selection of systems makes no claim to be representative, although it does span the whole size range for which we have data. (ii) For want of any ready alternative, the entries assume steady prelaunch acceleration. (iii) Accelerations not reported in the literature have been calculated from launch speeds and estimates (from body

proportions) of prelaunch travel distance. For mammals, with negligible drag, launch speeds come from jump heights; for smaller projectiles the computer program mentioned in the last essay was used to work back from reported ranges.

Before looking for relationships among these data, we might take note of the extreme accelerations of small projectiles. A *Pilobolus* sporangium, at $100,000 \text{ m s}^{-2}$, approaches the acceleration of a rifle bullet, typically $500,000 \text{ m s}^{-2}$. A *Gibberella* spore, at this point the biological record holder, accelerates at a truly cosmic $8,500,000 \text{ m s}^{-2}$. Indeed, the sheer diversity of organisms in the table makes us suspect that extraordinary accelerations might not require extraordinary engines.

Logarithmic graphs do lovely (and all too often misleading) service in suppressing scatter and the uncertainties introduced by rough estimates, especially where data span many orders of magnitude. Figure 1 gives such a log-log plot for the data just tabulated; a linear regression of the logarithms gives a slope of -0.86 . That scaling exponent comes reasonably close to a value of -1.0 especially when one considers the diversity of both organisms and engines. And including rhinos, polar bears, and other unlikely leapers among the big mammals would have offset the inclusion of some underperforming arthropods

and pushed the exponent still closer to -1.0 . Our forefathers have been vindicated – asserting that all creatures can jump to the same height implies a scaling relationship for acceleration quite close to what we find.

But that diversity ought to raise a flag of suspicion. Why should an argument based on muscle work for systems that do their work with other engines? Muscle represents no typical biological engine – it ranks at or near the top in, for instance, power-to-mass ratio.

Also, the scatter ought to be examined. Sub-par performance should raise few eyebrows, since fitness need not turn on personal ballistics. Less easy to rationalize are systems that do better than expected. One kind of seed, that of the tropical tree, *Hura crepitans*, clearly outguns all other ballistic seeds for which I have found data – it certainly deserves additional investigation. Seeds in general do better than arthropods of about the same size. A *t*-test supports that impression, yielding a significant difference between the size-acceleration products for the two groups (excluding *Hura*, the extreme outlier). Where sizes overlap, both arthropods and mammals do better than frogs. Despite Mark Twain's famous short story, frogs don't jump all that well – they're just sedentary creatures from which single long-jumps can be elicited easily.

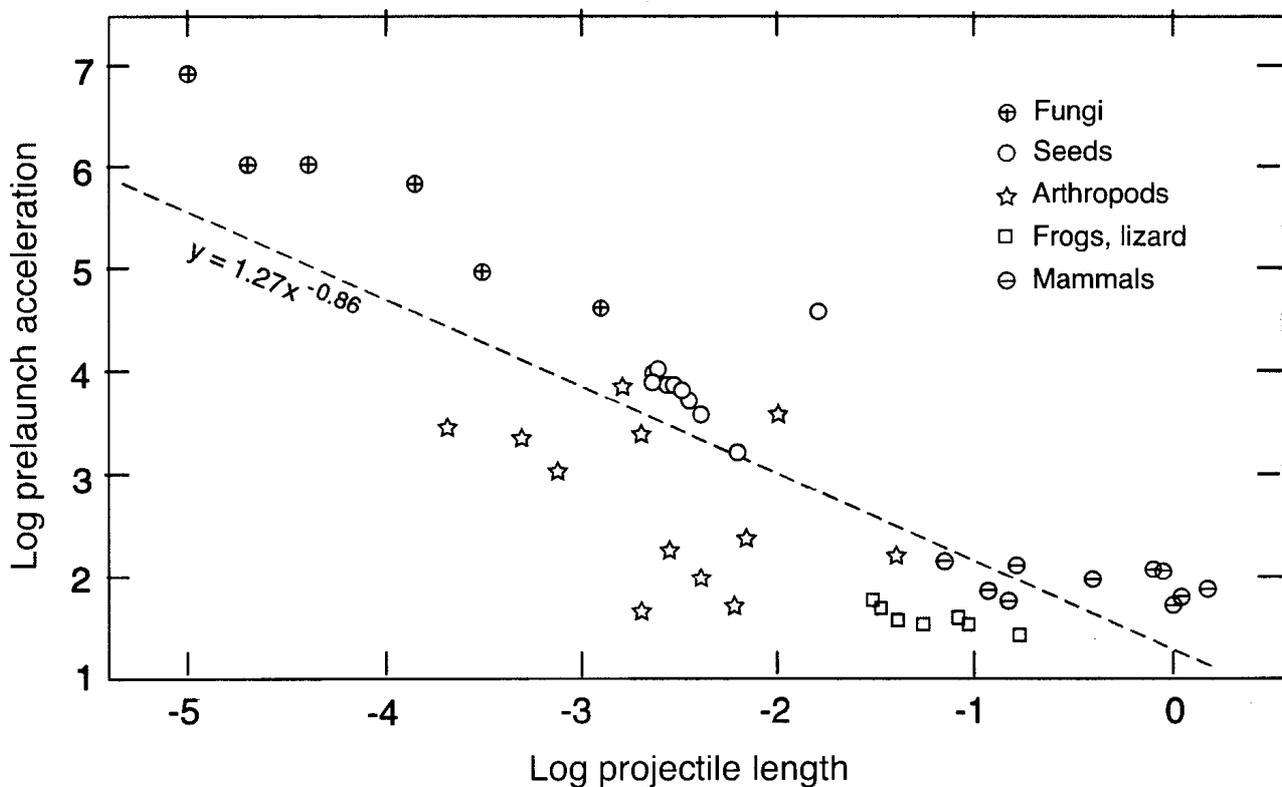


Figure 1. Projectile acceleration versus projectile size, with the linear regression line and equation for the data set. $r^2 = 0.671$.

3. The limitations of real engines

But we cannot conclude that the near-inverse proportionality confirms our reasoning. Something else must be afoot – again, the original argument presumed isometric muscle-powered jumpers – and we get the odour of a more powerful basis for the scaling of projectile performance. The way the original rationale brushes aside the sometimes extreme effects of aerodynamic drag received attention in the preceding essay. In addition, it sweeps aside both a serious biological limitation and a major physical presumption. These will be our present concerns.

The biological limitation comes from way muscle performance scales – or fails to scale. The work a muscle can do, relative to its mass, depends little on its size or that of its animal. But consider jumpers impelled upwards by muscles that shorten as they jump – shortening, as one might say, in real time. An invariant launch speed demands that the muscles of the smaller animal do their work in a shorter time.

Skeletal muscle differs only a little either from muscle type to muscle type or with animal size in our broad-brush view. The resting length of the basic contractile unit, the sarcomere, is about 2.5 μm in vertebrates, and it varies by less than an order of magnitude elsewhere if we exclude a few odd extremes. Muscles consist of sarcomeres in series, so if all sarcomeres shorten at the same speed, then contraction speed should be directly proportional to muscle length. Or speed relative to length, called ‘intrinsic speed’ and given in units of reciprocal seconds, should not vary with body size. (‘Intrinsic speed’, not a speed in the strict length-per-time sense, equals minus the ‘strain rate’, as usually used in the engineering literature; the change of sign reflects a shift from shortening during normal muscle action to stretch during a tensile test.)

Muscle does not operate with equal effectiveness over a wide range of intrinsic speeds; an individual muscle does not operate with equal effectiveness over a wide range of actual speeds. A muscle pulls most forcefully (ignoring pulling during imposed extension) when not shortening at all, at zero speed. Force then drops off with speed until it hits zero at some maximum speed. Power, force times speed, peaks at about a third of that maximum speed. (McMahon 1984 gives a particularly good discussion of such matters.) In short, both force and power peak at speeds well below maximum.

Making a small animal power its jump by real-time muscle contraction forces its muscles to operate at high intrinsic speeds, speeds that either imply reduced effectiveness or cannot be reached at all. For example, consider two animals with launch speeds of 5 m s^{-1} . One is 1.2 m high and has to get up to launch speed in a third of its height, or 0.4 m. Working backwards from launch speed and distance gives an acceleration time of 0.16 s

(and, incidentally, an acceleration of 31 m s^{-2}). It jumps, say, with muscles 0.3 m long that shorten by 20% of their length in the process, or 0.06 m. Thus its muscles shorten at a speed of 0.06 m/0.16 s or 0.375 m s^{-1} . Dividing by muscle length gives 1.25 s^{-1} as intrinsic speed, low enough to get a fine power output, perhaps a decent fraction of the 250 W kg^{-1} that approximates muscle’s practical maximum.

Contrast that with a similar animal a hundred times shorter, 12 mm. It must get up to speed in 1.6 ms (with an acceleration of 3100 m s^{-2}). Its 3-mm-muscles must shorten by 0.6 mm, thus at an identical speed of 0.375 m s^{-1} . Real-time muscle contraction of its shorter muscles takes a hundred-fold higher intrinsic speed, 125 s^{-1} , well beyond what vertebrate striated muscle can do. A mouse finger extender holds the upper record, 22 s^{-1} , but biological systems have difficulty getting reasonable (if suboptimal) outputs for power-demanding tasks above about 10 s^{-1} ; where peak power matters, 5 s^{-1} is hard to exceed.

Therefore the old argument that all animals can jump to the same height cannot be correct if based on real-time muscle work – the physical presumption mentioned earlier. At best the rationale works above the body length at which necessary intrinsic speed becomes limiting. Jumping ability ought to drop off for animals less than 50 to 100 mm long. And judging by actual performances, even above that length size still seems to count. Cougar and kangaroo have muscles that yield more work per contraction relative to their masses and can jump higher than can jerboa and kangaroo rat. Drag is not the culprit (as noted in the last essay); they do indeed have higher launch speeds.

4. Amplifying power

Almost all the smaller jumpers evade this limitation on muscular performance by using power amplifiers to reach their necessarily higher accelerations. After all, conservation of work or energy does not imply conservation of power for non-sustained tasks. A system need only apply energy slowly and then release it rapidly – as done in archery.

A look at some large, muscle-powered weapons provides as good a direct comparison as I know between devices lacking and equipped with power amplifiers. Prior to the advent of cannon, Medieval Europe and Asia attacked fortifications with first one and then another version of a catapult, the two devices called, respectively, traction trebuchets and counterweight trebuchets (Hill 1973), as shown in figure 2. A traction trebuchet applied power in real time – the artillerymen pulled simultaneously downward on one arm, raising the arm and projectile-bearing sling on the other side of the fulcrum. A counterweight trebuchet stored energy gravitationally – artillerymen pulled downward on the arm with the sling and projectile, slowly raising a weight (of as much as

10,000 kg) on the other end. Releasing a catch on the lowered arm allowed the counterweight to plummet, raising that arm with its sling and projectile. Combining historical information with a few assumptions, the performances of representative trebuchets of the two kinds can be calculated (Vogel 2001).

A traction trebuchet could throw a 60 kg mass a distance of 90 m, implying a launch speed of 30 m s^{-1} . A human can pull downward for a distance of a meter with a force of 220 newtons, doing 220 joules of work per pull. Since the projectile needs $1/2 \times 60 \times 30^2$ or 27,000 joules per shot, at least 120 artillerymen had to pull – assuming massless arms and other unlikely idealizations. At Sind, now in Pakistan, in 708 CE, 500 people reportedly worked a single weapon – about 50 joules per operator per shot.

A counterweight trebuchet could throw a 225 kg mass a distance of 260 meters and thus with a launch speed of 50 m s^{-1} and an energy of 300,000 joules per shot. Without power amplification that would have demanded about 1400 artillerymen, again assuming perfect efficiency. As best we can tell, only about 50 were so employed – an effective output of not 50 but 6000 joules per operator per shot.

The anatomically simplest power amplifier uses antagonistic muscles to preload some elastic component. In that way a jump can be powered by the combined energy of direct muscular action and of elastic recoil of energy put in earlier. Most or all of the vertebrates – and certainly all the smaller ones – listed in table 1 augment direct, real-time muscular action with some preloading of elastic components. The main storage sites are the tendons in series with the jumping muscles themselves. These complex muscle-tendon systems have yet to be fully analysed, but they appear to involve initial crouching counter-movements and some kind of catapult mechanism – at the least (Alexander 1988; Aerts 1998).

Calculations of the power outputs of jumping muscles often give values well above what isolated muscle can do – which, in the absence of more specialized devices, points to such preloading. A tree frog, *Osteopilus*, for instance, achieves a peak output in a jump about seven times higher than the maximum output of the muscles it uses (Peplowski and Marsh 1997); it may be extreme, but its power booster is not unique among frogs. With such amplification, frogs keep their intrinsic speeds fairly low, below about 5 s^{-1} (Marsh 1994). A jumping bushbaby (*Galago senegalensis*) does something similar; Aerts (1998) calculated that for direct action of leg extensors to power its jumps, those muscles would need to weigh twice that of the entire body. Frogs and bushbabies look like good jumpers, with big, specialized hind limbs. But little obvious structure underlies their power amplifiers – they seem to do their tricks the way an eager (and abusive) automobile driver races the engine before engaging the clutch or automatic transmission.

Power amplification appears almost universal among arthropods – only one group of jumpers clearly lack any specialized device. Despite the name, the salticid spiders do not jump especially well, at least by the criteria of launch speed and acceleration. Parry and Brown (1959) looked hard but found no amplifier. Spiders, though, are something of a law unto themselves, since they extend their legs with hydraulics rather than by direct muscular action.

Jumping with real-time muscle action or with simple preloading has its limits. Figure 3 fleshes out the picture presented by figure 1. A horizontal line seems to mark an upper limit for operating as do frogs, lizards, mammals, and salticid spiders. Nature, it appears, does not use real-time muscle action, even in mildly augmented form, as the main impetus for accelerations above about 150 m s^{-2} , whatever the size of creature or projectile. So we are

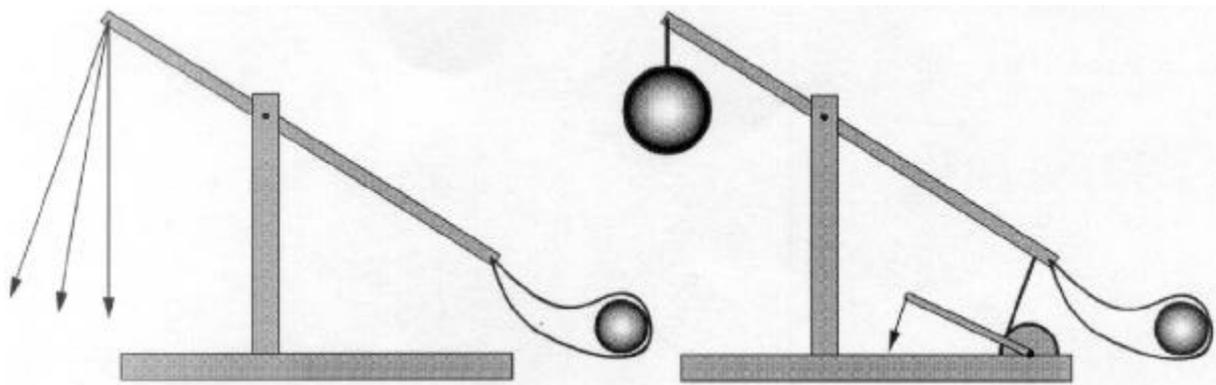


Figure 2. Diagrammatic versions of two large types of artillery powered by human muscle; both throw their projectiles from slings. The traction trebuchet, on the left, stored no energy except perhaps as kinetic energy of the moving arm; the counterweight trebuchet, on the right, made heavy use of gravitational storage.

left with the regression line in the figure with a slope (-0.86) close to (indeed, statistically indistinguishable from) the value predicted (-1.0) on the basis of an argument now revealed as specious, even for muscle-powered jumpers.

5. How to really amplify power

So far we have focused on muscle as engine. Again, both muscle's power relative to weight and speed relative to

size put it near the high end among living engines. Direct or largely direct powering of ballistic launches may be possible for muscular systems, at least for large ones. By contrast, where other engines drive launches, power amplification must be an absolute necessity for any kind of ballistic travel.

What, then, are the options for serious amplification? Linking a slow input with a rapid output requires a way to store energy. Our human technology employs such things as flywheels and rechargeable chemo-electric bat-

Table 1. Projectile sizes and estimates of prelaunch accelerations for biological projectiles.

Projectile		Length	Acceleration	Source
<i>Gibberella zeae</i> spore	f	0.00001	8,500,000	Trail <i>et al</i> (2005)
<i>Sordaria fimicola</i> , spore	f	0.00002	1,100,000	Ingold and Hadland (1959)
<i>Sordaria</i> , 8-spore cluster	f	0.00004	1,100,000	Ingold and Hadland (1959)
<i>Ascobolus immersus</i> , spores	f	0.00015	630,000	Fischer <i>et al</i> (2004)
Moss mite (<i>Zetorchestes</i>)	a	0.0002	3,400	Krisper (1990)
<i>Pilobolus</i> sporangium	f	0.0003	100,000	Buller (1909)
Rat flea	a	0.0005	2,000	Bennet-Clark and Lucey (1967)
Box moss mite (<i>Indotritia</i>)	a	0.0008	1,200	Wauthy <i>et al</i> (1998)
<i>Sphaerobolus</i> glebal mass	f	0.0012	46,000	Buller (1933)
<i>Geranium molle</i>	s	0.0016	8,100	Stamp and Lucas (1983)
Flea beetle (<i>Psylliodes</i>)	a	0.002	2,660	Brackenbury and Wang (1995)
Springtail	a	0.002	47	Brackenbury and Hunt (1993)
<i>Geranium carolinarium</i>	s	0.002	10,300	Stamp and Lucas (1983)
<i>Viola striata</i>	s	0.0021	7,800	Stamp and Lucas (1983)
<i>Ruellia brittoniana</i>	s	0.0023	10,000	Witztum and Schulgasser (1995)
<i>Vicia sativa</i>	s	0.0027	7,500	Garrison <i>et al</i> (2000)
Skipper butterfly frass	a	0.0028	180	Caveney <i>et al</i> (1998)
<i>Geranium maculatum</i>	s	0.0029	7,600	Stamp and Lucas (1983)
<i>Croton capitatus</i>	s	0.0035	5,200	Garrison <i>et al</i> (2000)
Froghopper	a	0.004	4,000	Burrows (2003)
Flea beetle (<i>Altica</i>)	a	0.004	100	Brackenbury and Wang (1995)
<i>Impatiens capensis</i>	s	0.0051	1,650	Stamp and Lucas (1983)
Salticid spider	a	0.006	51	Parry and Brown (1959)
Desert locust, 1st instar	a	0.007	200	Katz and Gosline (1993)
Click beetle	a	0.010	3,800	Evans (1972)
<i>Hura crepitans</i>	s	0.016	41,000	Swain and Beer (1979)
<i>Acris gryllus</i>	h	0.027	64	Marsh and John-Alder (1994)
<i>Pseudacris crucifer</i>	h	0.029	58	Marsh and John-Alder (1994)
Desert locust adult	a	0.040	160	Katz and Gosline (1993)
<i>Hyla squirella</i>	h	0.044	29	Marsh and John-Alder (1994)
<i>Hyla cinerea</i>	h	0.056	26	Marsh and John-Alder (1994)
Jumping mouse	m	0.07	143	Nowak (1991)
<i>Anolis carolinensis</i>	h	0.07	45	Toro <i>et al</i> (2003)
<i>Osteopilus septentrionalis</i>	h	0.088	26	Marsh and John-Alder (1994)
Jerboa, kowari, kangaroo rat	m	0.12	75	Nowak (1991)
Red squirrel	m	0.15	60	Essner (2002)
Lesser galago	m	0.16	140	Bennet-Clark (1977)
<i>Rana catesbiana</i>	h	0.164	20	Marsh (1994)
Potoroo	m	0.4	100	Nowak (1991)
Springbok	m	0.8	125	Nowak (1991)
Impala	m	1.0	100	(various)
Cougar (mountain lion)	m	1.0	55	Nowak (1991)
Gray kangaroo	m	1.1	67	Nowak (1991)
Horse, eland	m	1.7	80	Nowak (1991)

Lengths in meters; accelerations in m s^{-2} . To convert the latter to multiples of gravitational acceleration ("g's"), divide by 10. (f, fungus; s, seed; a, arthropod; h, frog or lizard; m, mammal.)

teries, schemes with only distant analogs in nature. Both human and natural technologies use gravitational storage – from counterweight trebuchets to pendulums in the former; stride-to-stride energy storage in legged walkers in the latter. One can imagine trees that toss fruit from wind-driven branches that sway as gravitational pendulums or seeds propelled by the drop of an elevated column of liquid, but I know no specific case of gravitational storage in biological ballistics. As far as I know, all pre-launch amplifiers depend on the same scheme, energy storage in deformed elastic materials.

Remind yourself of the simplicity and ubiquity of power amplification through brief elastic energy storage by flipping the nearest toggle switch, one that controls the room lights or some piece of household electronics. With most such switches, one pushes a lever with increasing force until it abruptly stops opposing your effort and switches to its alternative position. You have slowly loaded a spring, which then rapidly releases that energy to make a sudden and robust change of electrical contact. You may continue to push, but you do little additional work once the spring has shifted from absorbing to releasing energy.

A single-shot amplifier, as in most ballistic plants and fungi, can be self-destructive and thus even simpler than

a spring-assisted switch. The fungus *Pilobolus*, for instance, bears its sporangium atop a liquid-filled hyphal tube, as in figure 4a. An osmotic engine raises the pressure in the tube until the sporangium suddenly detaches along a specific junctional line and takes flight (Buller 1909). That commonest of fungal schemes gets tweaked by ones such as *Sordaria* that manage to avoid self-destruction long enough to loose a series of up to eight spores in quick succession (Ingold and Hadland 1959). Another fungus, *Sphaerobolus*, uses a one-shot catapult in which an initially concave cup ('peridium') containing a millimeter-wide glebal mass of spores suddenly everts, becoming convex upward (Buller 1933, figure 4b). A similar bistable system has recently been described by Forterre *et al* (2005) in a higher plant, the Venus's flytrap. In both fungi and flytrap, the ultimate engine is osmotic, coupled hydraulically with the output device.

Many seed shooters use another single-shot system, one in which drying of an initially hydrated structure such as a seed pod gradually stresses some woody (cellulosic) material. The movement accompanying breakage then sends the seed (or a group of seeds) onward. In *Ruellia*, for instance (figure 4c) sudden lengthwise rupture of the seam between two external valves (each analogous to a half-shell of a bivalve mollusk) lets the valves bend

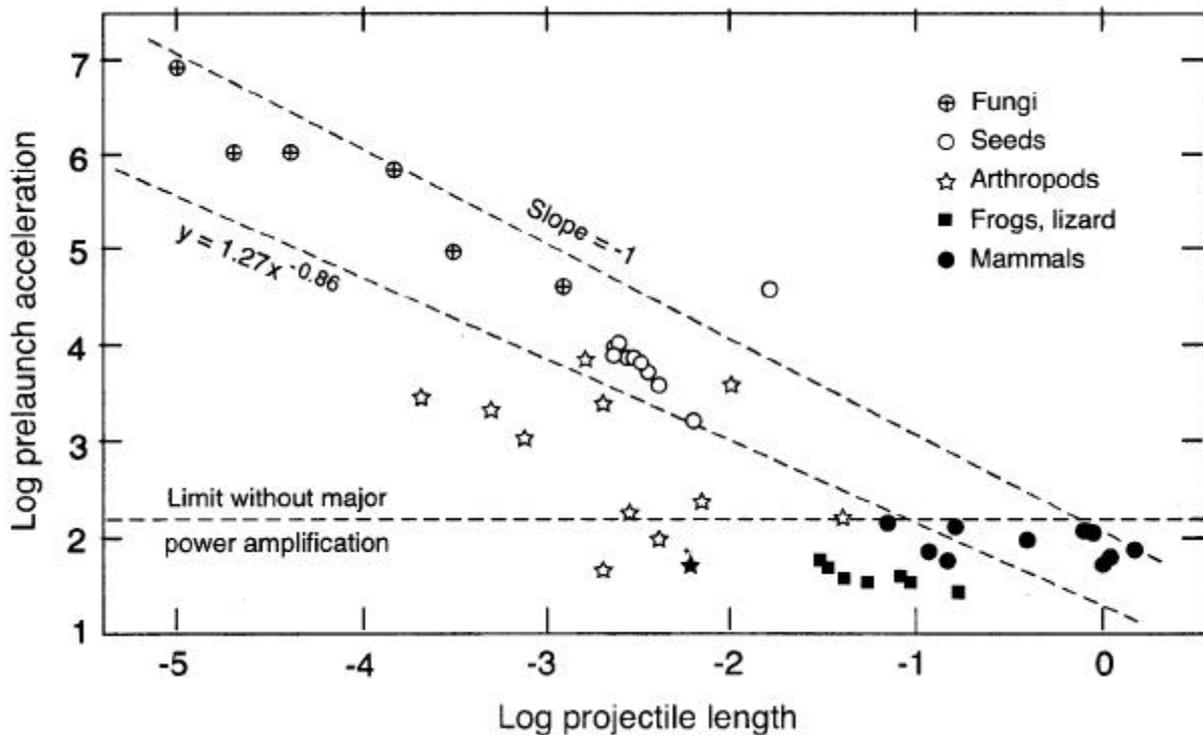


Figure 3. The same data and graphing conventions as in figure 1, but now showing which organisms make major use of elastic energy storage (solid symbols) and with an approximate performance limit line drawn on.

outward. That causes arms attached to the insides of valves to bend upward, whereupon each arm pushes a seed up and out (Witztum and Schulgasser 1995).

Among repetitive amplifiers, that of locusts and grasshoppers is especially straightforward. According to Bennet-Clark (1975), rather than directly powering a jump, the large extensor muscle of each hind tibia loads a pair of elastic elements. A catch near the junction of the (proximal) femur and (distal) tibia keeps the leg flexed – a jump must start with fully flexed tibias. Relaxation of the flexor muscle releases the catch, and the immediate power for the jump comes mainly from energy stored in the chitin of elastic cuticle. The peak power output of 0.75 watts from 70 mg of muscle represents almost $11,000 \text{ W kg}^{-1}$, around 40 times what muscle can do directly. Moreover, amplification permits locust jumping muscle to operate at an efficiently low intrinsic speed, peaking at less than 2 s^{-1} .

Fleas (Bennet-Clark and Lucey 1967) have a more intricate mechanism, about which I will give even less detail. A rabbit flea requires about 100 ms for the large trochanteral depressor muscles of its hind legs to deform a pair of elastic pads, here not chitin but the softer and spectacularly resilient protein resilin. A second pair of muscles trigger energy release by moving a strap sideways, undoing the catch. The jump itself lasts only 0.7 ms,

quicker by nearly 150 times. Energy storage permits the muscles to operate at a very forceful intrinsic speed of 0.55 s^{-1} rather than an impossible 50 s^{-1} or more.

6. Storing energy elastically

Table 2 compares the key properties of several of the materials available for elastic energy storage, with spring steel included for reference. Of course ancestry constrains the choice of energy storage material. Thus only arthropods make resilin, and cellulose mainly occurs in plants. And the storage materials of most projectile-producers represent only mild modifications of those of non-projectile-producing forebears. For resilience, work regained relative to work put in, resilin, known best from insect wing hinges, beats any other biological material. It may have to be superb, not because a few percent gain in resilience matters much to fitness, but because the loss relative to perfect resilience (1.0) appears as heat, something not well tolerated in insect wing hinges, where it may be alternately stressed and released hundreds of times each second. Fleas just happen to be in an auspicious lineage.

Tendon is mainly collagen, our main elastic energy store (the protein elastin plays a lesser role); it also does

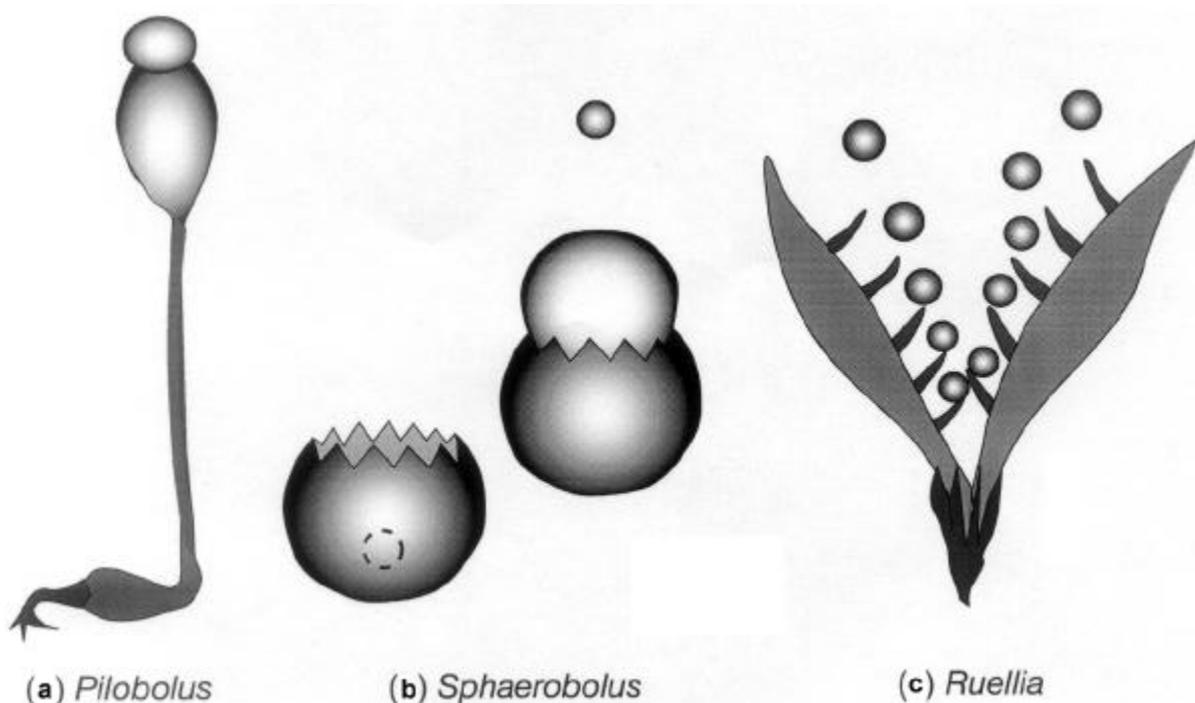


Figure 4. The diverse launching devices of three ballistic organisms. The fungus *Pilobolus*, is shown with the sporangium on top of the subsporangial swelling just before it shoots upward on a jet of cell sap. *Sphaerobolus* appears just before and just after a glebal mass of spores gets sent aloft by eversion of the floor of the cup. The seed *Ruellia* has been caught just before the end of launch, with each seed propelled upward by motion of the ejaculator beneath it.

well but has quite a different character and has to be used differently. Resilin, softer (elastic modulus 1.9 MN m^{-2}), can be usefully loaded in compression or shear. Collagen, stiffer (modulus $1,500 \text{ MN m}^{-2}$) works best in tensile applications, and even there it cannot be arranged like a conventional rubber – it operates at high forces and low extensions, crucial when linking muscles to bones.

Wood, despite our long use of wooden bows for archery, has poor resilience – we take advantage of its internal damping to get mellifluous resonators in many musical instruments. But woods vary widely (as instrument makers have long known), and fresh wood can be quite different from dry stuff. We know very little about the storage capabilities and resilience of woods (and other cellulosic materials) as used for energy accumulation and release in nature's ballistic devices. On the one hand, ballistic seeds do impressively well, suggesting high resilience. On the other hand, the structures involved represent a tiny fraction of the total mass of a plant and probably an even smaller fraction of its lifetime energy expenditure, so efficiency relative to either mass or work might not matter. We know still less about the properties of the materials that fungi use for energy storage.

Air makes a perfectly fine elastic material, taking loads in either compression (almost without limit) or tension (at least to $101,000 \text{ N m}^{-2}$, one atmosphere). I know of no case of its use in any ballistic system in nature, although I suspect that a moss, *Sphagnum*, might store energy for spore ejection by compressing air, as noted in the last essay. Water, by its ubiquity and the data in the table, looks attractive; but that proves illusory. Its extremely low compressibility (or high bulk modulus, the same thing) produces an awkward mismatch with biological solids. Squeeze water in a container of any such solid and the container stretches more than the water compresses – water requires operation at extremely high force with extremely low volume change. So, while water makes a superb medium for transmitting hydrostatic pressures, it turns out to be next to useless for storing energy.

The final column of the table 2 gives a severely idealized calculation of the minimum mass of elastic material relative to the weight of the projectile. In essence, it equates the initial kinetic energy of the projectile with the product of (i) the work (energy) of extension relative to mass of the elastic, (ii) the resilience of the elastic, and (iii) the mass of the elastic. The assumed launch speed of 5 m s^{-1} corresponds to a dragless vertical ascent of 1.25 m – a typical value for the present systems. On this perhaps biased basis, the biological materials look remarkably good.

7. What does limit acceleration and launch speed?

The old argument has been shredded. The work relative to mass of a contracting muscle deteriorates as animals get smaller rather than holding constant – a consequence of the requisite rise in intrinsic speed. Muscle need not and commonly does not power jumps in real time – elastic energy storage in tendons of collagen, in apodemes of chitin, and in pads of resilin provides power amplification. Finally, muscle powers none of those seeds and tiny fungal projectiles. Yet acceleration persists in scaling as the classic argument anticipates.

A look at the properties of elastic materials dispels any notion that their ability to store energy imposes a particular limit. Even the extreme case, launching a *Hura* seed with the energy of stretched or squeezed wood, would take an elastic mass only 5 or so times the mass of the projectile. That volume of elastic should be no problem, at least for shooters rather than jumpers. Distance (and thus speed) amplifying levers can compensate for inadequate speed of recoil of an elastic. And nature could probably enlarge muscular systems or run osmotic engines at higher pressures (although Alexander 2000 gives an argument against the first of these).

A possible alternative emerges from reexamination of the relationship between force and acceleration. If acceleration indeed scales inversely with length and mass di-

Table 2. The relevant properties of materials for brief elastic energy storage and release (Bennet-Clark 1975; Gosline *et al* 2002; Jensen and Weis-Fogh 1962; Vogel 2003). The numbers presume an uncomfortably large number of assumptions about such things as operating conditions and ignore large elements of biological variability.

Material	Energy/volume	Energy/mass	Resilience	Relative elastic mass
Arthropod cuticle	9.6 MJ m^{-3}	$8,000 \text{ J kg}^{-1}$	~ 0.8	$\sim 0.2\%$
Tendon (collagen)	2.8	2,500	0.93	0.54
Wood	0.5	900	~ 0.5	~ 2.3
Resilin	1.5	1,250	0.96	1.04
Spring steel	1.0	150	0.99	8.42
Air	0.000500	417	1.00	0.75
Liquid water	0.18	180	1.00	6.94

rectly with the cube of length, then force should scale with the square of length. Or, put another way, force divided by the square of length should remain constant. Force over the square of length corresponds to stress. Perhaps our empirical finding that acceleration varies inversely with length tells us that stress in some manner limits these systems. A stress limit would represent no great biological novelty, having been recognized (or invoked) in remodelling of bone, resizing of blood vessels, and the growth of trees (see, for references, Vogel 2003).

The stress limit may go well beyond the maximum pull of a muscle. It might reflect a point of self-destruction, a limit that the propulsive equipment of a system might exceed only at risk, one might say, to life and limb. That could apply even to the largest jumpers, since experimental work on humans – anticipating rocket launches – shows that our bodies do not take kindly to accelerations much above those experienced by large mammalian jumpers. It also rationalizes the greater accelerations of seeds than of arthropods – seeds, simpler and sturdier, should be less easily damaged by high launch accelerations. I have to pick up small insects carefully lest I damage them; seeds I grind in mortar with pestle. (Of course seeds are not self-propelled, the basis of an alternative explanation.)

Figure 3 has one further line, a line with a slope of -1 over its more than five orders of magnitude of size. It has been drawn so it roughly follows the extremes of acceleration (that eccentric seed of *Hura* is again an outlier). Maybe that line is the important one, a practical constraint imposed by the materials and structures of biological projectiles that must not be rendered dysfunctional by their ballistic episodes – these are whole animals and propagules, not bullets. That limit line, reflecting the scaling of force with the square of length, might be pointing to the size-independence of maximum stress tolerable by biological materials. It is consistent with (and may reduce to an example of) a more general scaling rule. Marden and Allen (2002) found just such scaling in the force output of a wide range of engines, ranging from molecular motors of myosin, kinesin, dynein, and RNA polymerase, through muscles to winches and rockets – their ‘group 1 motors’ – and attribute it to a common limit on just this capacity to withstand mechanical stress.

Several final notes: The present essay, following its predecessor, has focused on projectiles. Other biological systems achieve high accelerations, and these accelerations also vary inversely with size, despite their diversity of propulsive engines. So, for completeness, I ought to mention the ejectable nematocysts of the coelenterates, the retractable spasmoneme of vorticellid protozoa, and the protrusible tongues of many amphibians and reptiles.

The homogeneity of the seeds (one again omitting *Hura* and thus emphasizing its aberrant character) rela-

tive to the other groups comes as a surprise. These ballistic seeds span a notably narrow size range, with lengths ranging from just under 2 mm to just over 5 mm, and their accelerations vary only slightly more. Other explosively discharged seeds, such as those studied by Stamp and Lucas (1990) appear to fit into the same cluster. One suspects some as yet unidentified constraint.

And then we return to that assertion about all animals jumping to the same height. J B S Haldane attributed it to Galileo; I believe he erred. I can find no such assertion or anything closer to it than his comment on the scaling of bones. I confirm D’Arcy Thompson’s attribution to Borelli, down to chapter and verse. Borelli was only translated into English long after Thompson wrote *On Growth and Form*; but, as an accomplished classical scholar, Thompson would have read Borelli in the original Latin.

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References

- Aerts P 1998 Vertical jumping in *Galago senegalensis*: the quest for an obligate mechanical power amplifier; *Philos. Trans. R. Soc. London* **B353** 1607–1620
- Alexander R McN 1988 *Elastic mechanisms in animal movement* (Cambridge: Cambridge University Press)
- Alexander R McN 2000 Hovering and jumping: contrasting problems in scaling; in *Scaling in biology* (eds J A Brown and G B West (Oxford: Oxford University Press) pp 37–50
- Bennet-Clark H C 1975 The energetics of the jump of the locust *Schistocerca gregaria*; *J. Exp. Biol.* **63** 53–83
- Bennet-Clark H C 1977 Scale effects in jumping animals; in *Scale effects in animal locomotion* (ed.) T J Pedley (London: Academic Press) pp 185–201
- Bennet-Clark H C and Lucey E C A 1967 The jump of the flea: a study of the energetics and a model of the mechanism; *J. Exp. Biol.* **47** 59–76
- Borelli G A 1680 *De motu animalium*; P Maquet, trans 1989 as *On the movement of animals* (Berlin: Springer-Verlag)
- Brackenbury J and Hunt H 1993 Jumping in springtails: mechanism and dynamics; *J. Zool. London* **229** 217–236
- Brackenbury J and Wang R 1995 Ballistics and visual targeting in flea-beetles (Alticinae); *J. Exp. Biol.* **198** 1931–1942
- Buller A H R 1909 *Researches on fungi* vol. 1 (London: Longmans, Green)
- Buller A H R 1933 *Researches on fungi* vol. 5 (London: Longmans, Green)
- Burrows M 2003 Froghopper insects leap to new heights; *Nature (London)* **424** 509
- Caveney S, McLean H and Surry D 1998 Faecal firing in a skipper caterpillar is pressure-driven; *J. Exp. Biol.* **201** 121–133
- Essner R L 2002 Three-dimensional launch kinematics in leaping,

- parachuting and gliding squirrels; *J. Exp. Biol.* **205** 2469–2477
- Evans M E G 1972 The jump of the click beetle (Coleoptera, Elateridae): a preliminary study; *J. Zool. London* **167** 319–336
- Fischer M, Cox J, Davis D J, Wagner A, Taylor R, Huerta A J and Money N P 2004 New information on the mechanism of forcible ascospore discharge from *Ascobolus immersus*; *Fungal Genet. Biol.* **41** 698–707
- Forterre Y, Skotheim J M, Dumais J and Mahadevan L 2005 How the Venus flytrap snaps; *Nature (London)* **433** 421–425
- Garrison W J, Miller G L and Raspet R 2000 Ballistic seed projection in two herbaceous species; *Am. J. Bot.* **87** 1257–1264
- Gosline J, Lillie M, Carrington E, Guerette P, Ortlepp C and Savage K 2002 Elastic proteins: biological roles and mechanical properties; *Philos Trans. R. Soc. London* **B357** 121–132
- Haldane J B S 1926 On being the right size; *Harper's Monthly* **152** 424–427
- Hill A V 1938 The heat of shortening and dynamic constants of muscle; *Proc. R. Soc. London* **B126** 136–195
- Hill D R 1973 Trebuchets; *Viator* **4** 99–114
- Ingold C T and Hadland S A 1959 The ballistics of *Sordaria*; *New Phytol.* **58** 46–57
- Jensen M and Weis Fogh T 1962 Biology and physics of locust flight. V. Strength and elasticity of locust cuticle; *Philos. Trans. R. Soc. London* **B245** 137–169
- Katz S L and Gosline J M 1993 Ontogenetic scaling of jump performance in the African desert locust (*Schistocerca gregaria*); *J. Exp. Biol.* **177** 81–111
- Krisper G 1990 Das Sprungvermögen der mitbengattung *Zetorchestes* (Acarida, Oribatida); *Zool. Jb. Anat.* **120** 289–312
- Marden J H and Allen L R 2002 Universal performance characteristics of motors; *Proc. Natl. Acad. Sci. USA* **99** 4161–4166
- Marsh R L 1994 Jumping ability of anuran amphibians; *Adv. Vet. Sci.* **B38** 51–111
- Marsh R L and John-Alder H B 1994 Jumping performance of hybrid frogs measured with high-speed cine film; *J. Exp. Biol.* **188** 131–141
- McMahon T A 1984 *Muscles, reflexes, and locomotion* (Princeton: Princeton University Press)
- Nowak R M 1991 *Walker's mammals of the world* 5th edition (Baltimore: Johns Hopkins University Press)
- Parry D A and Brown R H J 1959 The jumping mechanism of salticid spiders; *J. Exp. Biol.* **36** 654–664
- Peplowski M M and Marsh R L 1997 Work and power output in the hindlimb muscles of Cuban treefrogs *Osteopilus septentrionalis* during jumps; *J. Exp. Biol.* **200** 2861–2870
- Stamp N E and Lucas J R 1983 Ecological correlates of explosive seed dispersal; *Oecologia (Berlin)* **59** 272–278
- Stamp N E and Lucas J R 1990 Spatial patterns and dispersal distances of explosively dispersing plants in Florida sandhill vegetation; *J. Ecol.* **78** 589–600
- Swaine M D and Beer T 1977 Explosive seed dispersal in *Hura crepitans* L. (Euphorbiaceae); *New Phytol.* **78** 695–708
- Thompson D'A W 1942 *On growth and form* (Cambridge: Cambridge University Press)
- Toro E, Herrel A, Vanhooydonck B and Irschick D J 2003 A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean lizards; *J. Exp. Biol.* **206** 2641–2652
- Trail F, Gaffoor I and Vogel S 2005 Ejection mechanics and trajectory of the ascospores of *Gibberella zeae* (anamorph *Fusarium graminearum*); *Fungal Genet. Biol.* (in press)
- Vogel S 2001 *Prime mover: a natural history of muscle* (New York: W W Norton)
- Vogel S 2003 *Comparative biomechanics: life's physical world* (Princeton: Princeton University Press)
- Vogel S 2005 Living in a physical world II. The bio-ballistics of small projectiles; *J. Biosci.* **30** 167–175
- Wauthy G, Leponce M, Banaï N, Silin G and Lions J C 1998 The backward jump of a box moss mite; *Proc. R. Soc. London* **B265** 2235–2242
- Witztum A and Schulgasser K 1995 The mechanics of seed expulsion in Acanthaceae; *J. Theor. Biol.* **176** 531–542

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