

## Living in a physical world II. The bio-ballistics of small projectiles

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### 1. Introduction

Many animals jump; many plants shoot their seeds. While ‘many’ may not imply ‘most’, terrestrial life is rife with examples of ballistic motion, motion in which a projectile gets all of its impetus prior to launch.

For most of us, the trajectories of projectiles appeared briefly early in a basic physics course. Some tidy equations emerged in unambiguous fashion from just two facts. A projectile moves horizontally at constant speed; only the downward acceleration of gravity ( $g$ ) alters its initial vertical speed. Where launch and landing heights are the same, a simple formula links range ( $d$ ) with launch speed ( $v_o$ ) and projection angle ( $Q_o$ ) above horizontal:

$$d = \frac{v_o^2 \sin 2Q_o}{g} . \quad (1)$$

So, for a given initial speed, a projectile achieves its greatest horizontal range when launched at an upward angle of  $45^\circ$ . That maximal range is simply

$$d_{\max} = \frac{v_o^2}{g} . \quad (2)$$

Thus an initial speed of  $40 \text{ m s}^{-1}$  ( $144 \text{ km h}^{-1}$ ) could take a projectile 163 m. Enroute, the projectile reaches a maximum height,  $h_{\max}$ , of a quarter of that best range, or

$$h_{\max} = \frac{v_o^2}{4g} . \quad (3)$$

The trajectory forms a nicely symmetrical parabola, and the loss of range at angles above  $45^\circ$  exactly mirrors the loss at lower angles – as shown in figure 1. Such tidiness gives (as once said) the biologist severe physics-envy.

In promoting these expressions, text or teacher may mutter, *sotto voce*, something about an assumed absence of air resistance, about the presumption that drag exerts a negligible effect.

Nevertheless the scheme generates significant errors even for a cannon ball. It gives still worse errors for golf balls – drag can halve the range of a well-driven golf ball (Brancazio 1984). The errors are tolerable only because golfers, however fanatic, rarely turn for help to physics. What keeps a projectile going is inertia; whether we view its consequences in terms of momentum or kinetic energy, mass provides the key element. Ignoring, to take a broad-brush view, variation in both density and shape, mass follows volume. What slows a projectile are two factors, gravity and drag. The standard equations deal with the downward force of gravity and produce their nice parabolas. Drag, the force that acts opposite the direction of motion, manifests itself in deviations from such simple trajectories; its magnitude varies in proportion either to surface area or diameter, depending on the circumstances. The smaller the projectile, the greater are both surface area or diameter relative to volume. So the smaller the projectile the less adequately that idealized, dragless trajectory should describe its motion. Since gravitational force, kinetic energy, and momentum all depend on mass, the less dense the projectile, the greater will be the relative influence of drag.

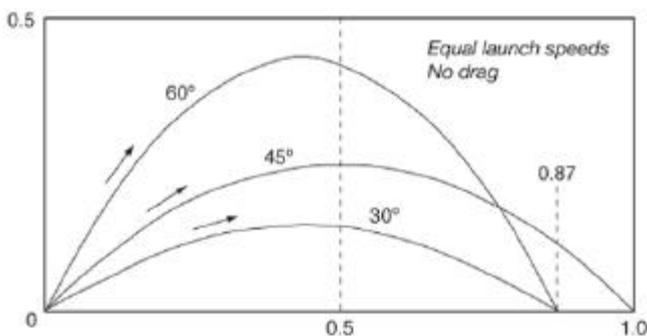
The upshot is that biological projectiles will be poorly served by these simple equations. Few are very large and none very dense, so their performances pale besides those of long-travelling and damage-inducing chunks of rock or iron. Still, life’s projectiles are diverse in ancestry, size, and function. Sports, hunting, and warfare, uses that come first to mind, matter least often to species other than our own. Instead, two functions dominate. Some organisms jump, forming single, whole-body projectiles; others shoot propagules – fruits, seeds, spore clusters, even individual spores.

### 2. Dealing with drag

In short, to look with any degree of realism at the trajectories of biological projectiles, we must, so to speak, put

drag into the equation. As it happens, that turns out to be trickier than one might expect. We biologists imagine a physical world run according to straightforward (if sophisticated) rules, at least when compared with the messy scene that evolution generates. The drag, at least of a simple object such as a sphere, ought to behave with predictable lawfulness rather than with our eccentric awfulness; one should be able to look up a basic equation for drag versus speed or drag versus size. Not so! Within the range of speeds and sizes that might matter to organisms, these are distinctly ill-tempered functions. The trouble traces to changes, sometimes abrupt, in how fluids flow over objects, whether laminar or turbulent, whether surface-following or separated, and so forth. For a large object going at a fairly high speed, drag varies with the square of speed and the area of the object. For a small object going slowly, drag varies with speed itself and the length of the object. In between, the relationship bears no resemblance to anything that might tempt use of our customary regressions and power laws.

Fortunately, two twentieth-century accomplishments save the day. First, from direct measurements we know how drag varies with speed and size for ordinary objects such as spheres moving through ordinary fluids such as air and water. And, second, even the most minimal desktop computer now makes short work of calculating draggy trajectories by an iterative approach. One starts with a projectile of a given size, density, launch speed ('muzzle velocity' in the common parlance of these violent times), and launch angle. After a short interval, the computer informs us of the projectile's slightly different speed and path, the two altered by gravity, acting downward, and drag, acting opposite the projectile's direction. The computer then takes the new speed and path as inputs and repeats the calculation to get yet another speed and path. In the simplest case, the computer stops iterating when



**Figure 1.** Without drag, trajectories are perfectly parabolic, with descent speeds and angles equal to ascent speeds and angles. For a given initial speed, maximum range occurs with a launch angle of 45°; ranges after either 30° or 60° launches are 87% of that maximum.

the projectile's height has returned to that of its launch – when it has returned to the ground.

The way drag gets into the picture, though, takes a little explanation. We normally express drag in dimensionless form, as the so-called drag coefficient,  $C_d$ . It amounts to drag ( $D$ ) relative to area ( $S$ ) divided by a kind of idealized pressure, that which would push on something were the fluid coming directly at it to effect a perfect transfer of momentum and then obligingly (and quite unrealistically) disappear from the scene. Specifically,

$$C_d = \frac{D/S}{\rho v^2/2}, \quad (4)$$

where  $\rho$  is fluid density and  $v$  is the speed of the object through the fluid. The commonest reference area is the maximum cross section of the object normal to flow, the area facing the oncoming fluid. Unfortunately, the relationship between speed and drag coefficient behaves no better than that between speed and drag itself – the equation just dedimensionalizes drag. If drag were simply proportional to area, fluid density, and the square of velocity, then  $C_d$  would be constant (and unnecessary). So variation in  $C_d$  exposes the eccentricities of drag. And  $C_d$  depends, not only on shape, but on the object's size and on the fluid's viscosity (where, but often  $h$ ) and density.

Fortunately, these last three variables operate as a particular combination, the dimensionless Reynolds number, mentioned in the previous essay,

$$Re = \frac{\rho l v}{\mu}, \quad (5)$$

where flow-wise length provides the commonest reference,  $l$  (Vogel 2004). Again,  $Re$  represents the ratio of inertial to viscous forces as fluid crosses an immersed object. Untidy still, but now one needs to know only how drag coefficient varies with Reynolds number and all the other relationships follow, at least for a given shape.

For present purposes, this last function,  $C_d = f(Re)$ , breaks into three separate domains. When  $Re$  exceeds 100,000, (again assuming a sphere)  $C_d = 0.1$ . For  $Re$ 's between 1,000 and 100,000,  $C_d = 0.5$ . Thus for both domains, drag varies with the square of speed, but with different constants of proportionality. For Reynolds numbers below 1,000, the best encapsulation I have seen comes from White (1974):

$$C_d = \frac{24}{Re} + \frac{6}{1 + Re^{1/2}} + 0.4. \quad (6)$$

(The first term on the right represents Stokes' law, trustworthy at Reynolds numbers below about one.) The computer need only decide, for each iteration, which of the approximations to apply.

Such a program gives all the important characteristics of a realistically draggy trajectory, starting with a projectile's size, density, launch angle, and launch speed – range, maximum height, impact angle, and impact speed. Looking at the computation point by point gives the shape of the trajectory. With only a little playing around one can work back from an observed range to a launch speed. Of course, the scheme assumes spherical projectiles, but most non-streamlined objects can be reasonably approximated as spheres of the same (or a little greater) volume. A version of such a program can be found in Appendix 2 of Vogel (1988).

For an initial example, consider a cannon and its projectile – a particular one whose barrel (on a new carriage) graces Edinburgh Castle for the delectation of tourists. James II of Scotland took delivery in 1457 of the weapon, called 'Mons Meg' after Mons, Belgium, where it was produced and an anonymous Meg (or Margaret). While too heavy to be of much use as a transportable siege weapon, apparently it could throw stone spheres half a meter in diameter about 3000 m. Assuming a typical density for stone ( $2700 \text{ kg m}^{-3}$ ), the computer program yields a launch speed of  $180 \text{ m s}^{-1}$  and a launch angle for maximum range (for that speed) of about  $43^\circ$ , a shade lower than the dragless  $45^\circ$ . No longer do the ranges at  $30^\circ$  and  $60^\circ$  match; now the  $30^\circ$  range wins by about 4%. Drag drops the best range of the projectile to 85.9% of the dragless,  $45^\circ$  calculation – we might say that it incurs a 'drag tax' of 14.1%. The difference would certainly have mattered – if the cannon could have been accurately aimed and ranged. So the simple formulas we were taught fall short (long, really) even where we thought they applied.

### 3. Playing games with balls

As suggested earlier, drag bothers a well-driven golf ball. If dragless, an initial speed of  $60 \text{ m s}^{-1}$  ( $216 \text{ km h}^{-1}$ ) would take it 365 m. Drag reduces that to 243 m, a tax of no less than 35.3%; that maximal range occurs with a launch angle of  $41.5^\circ$ . That noticeably distorts the standard parabola, with a descent a bit steeper than the preceding ascent and with a landing speed a little below launch speed. Is this result general for the balls we use in our various sports?

One might guess that a basketball, larger and less dense, would suffer relatively more from drag. But in practice its lower speed and thus relatively low drag ( $D$ , of course, not  $C_d$ ) mitigates the problem. For a launch speed of  $20 \text{ m s}^{-1}$  ( $72 \text{ km h}^{-1}$ ) it goes 35.7 instead of 40.7 m, losing only 12.3%. And the best launch drops only a little below  $45^\circ$ , to  $43.5^\circ$ . A well-kicked football (in North America, a soccer ball) goes faster than a thrown basket-

ball; unsurprisingly, its susceptibility to drag lies between those of golf and basketballs. A launch speed of  $30 \text{ m s}^{-1}$  ( $108 \text{ km h}^{-1}$ ) takes it 67.6 m instead of 91.6 m, a tax of 26.1%, with the best distance achieved with a launch angle of about  $43^\circ$ . Basketballs and footballs have about the same sizes and overall densities – launch speed determines the difference. For none of these, though, does drag amount to more than a secondary factor.

Since so much in fluid mechanics depends on the Reynolds number, we might examine the present values for projectiles at launch. For the cannonball,  $Re = 6,000,000$ ; for the football, 440,000; for the basketball, 320,000; for the golf ball, 170,000. Clearly Reynolds number alone provides no easy key to the importance of drag. Nor does what we have called the drag tax depend in any direct fashion on launch speed. We will revisit the way the effect of drag on trajectories might be predicted in a few pages.

### 4. Where drag matters little for organisms . . .

First, though, we should examine existing data for biological projectiles, taking advantage of the computer to estimate launch speed from range and vice versa. Such data exist for a wide variety of systems – the present account will be selective rather than exhaustive. Together with those for the preceding cases, input data and results are summarized in table 1. Consider, to start with, a small, jumping mammal, a species of kangaroo rat (*Dipodomys spectabilis*) native to western North America and similar to the jerboa of North Africa and the marsupial kowari of Australia. It can be approximated as a sphere about 0.1 m in diameter with a density of about  $750 \text{ kg m}^{-3}$ . According to Biewener *et al* (1981), it can hop along bipedally at up to  $3.1 \text{ m s}^{-1}$  ( $11.2 \text{ km h}^{-1}$ ), which implies a launch speed (above the horizontal, of course) of about  $3.1/\sin 45^\circ$  or  $4.4 \text{ m s}^{-1}$  ( $15.8 \text{ km h}^{-1}$ ). It achieves its best performance at a launch angle indistinguishable from  $45^\circ$  and incurs a drag tax of only about 1.1%. Why so little effect? Mainly, as we saw for the basketball, its decent size and thus fairly high mass together with its low launch speed and thus relatively low drag.

Among mammals that make haste with bipedal hopping, kangaroo rats are among the smallest. Simple consideration of surface-to-volume ratio – or, in effect, drag-to-gravity ratio – tells us that larger mammals will suffer even less from drag. So we anticipate that neither control of body posture, streamlining, nor altered piloerection will make much difference either to range, best launch angle, or speed. Where shape and postural changes do matter are among animals that glide, where lift-to-drag ratio plays a crucial role, and among animals that 'parachute', deliberately increasing drag to lower falling speeds.

Similarly, drag should not be a significant factor for any fair-sized animal that locomotes with a sequence of short ballistic trajectories – one that goes arm-over-arm, brachiating from hand-hold to hand-hold (see, for instance, Usherwood and Bertram 2003). Nor will it matter for those amphibians that throw their prehensile tongues forward as prey-capturing devices, despite their impressive performances – the tongue of *Bufo marinus*, a large toad, accelerates at over 30 times gravity to launch at nearly  $3 \text{ m s}^{-1}$  ( $10.8 \text{ km h}^{-1}$ ) (Nishikawa and Gans 1996); that of the salamander *Hydromantes imperialis* extends by 80% of its body length (Deban *et al* 1997). Nor does drag make a great difference for a yet odder practitioner of ballistics. At least one insect lineage shoots fecal pellets, apparently to minimize their potential predator-directing role (Weiss 2003). The pellets of a skipper caterpillar, *Calpodex ethlius*, average 2.8 mm in diameter and about  $930 \text{ kg m}^{-3}$  in density. After launch at  $1.6 \text{ m s}^{-1}$  ( $5.8 \text{ km h}^{-1}$ ) they go about 0.246 m, only 5.4% below their dragless range, achieved at  $1^\circ$  below the dragless  $45^\circ$  angle (input data from Caveney *et al* 1998). The pellets may be on the small side, but they do not go fast.

### 5. Smaller jumpers

As the size of jumpers drops, drag becomes increasingly important, as one can see from table 1. A desert locust (*Schistocerca gregaria*) can be approximated as a 10 mm sphere of  $500 \text{ kg m}^{-3}$  density; a launch speed to  $3.0 \text{ m s}^{-1}$

( $10.8 \text{ km h}^{-1}$ ) takes it about 0.85 m downrange, 6.1% less than its dragless range (data from Bennet-Clark 1975). So it does only a bit worse than a skipper's pellet.

A particular froghopper or spittle bug (*Philaenus spumarius*), smaller than a locust (about 4 mm in diameter), takes advantage of a slightly faster launch,  $4.0 \text{ m s}^{-1}$  ( $14.4 \text{ km h}^{-1}$ ), to go farther, about 1.22 m, in the process, though, suffering a worse loss of range, 25.0% to drag and doing best at  $42^\circ$  (data from Burrows 2003).

A flea beetle (*Psylliodes affinis*), still smaller (about 1.6 mm), has a similar, if a bit lower, initial speed,  $2.93 \text{ m s}^{-1}$  ( $10.5 \text{ km h}^{-1}$ ); the latter takes it less far, 0.543 m, but with a worse drag tax, 37.9%. It gets its best range at a launch angle of  $40^\circ$  (data from Brackenbury and Wang 1995).

Fleas, smaller yet, encounter far greater trouble with drag. According to Bennet-Clark and Lucey (1967), a rabbit flea (*Spilopsyllus cuniculatus*) about 0.5 mm in diameter takes flight at  $4.0 \text{ m s}^{-1}$  ( $14.4 \text{ km h}^{-1}$ ). Drag reduces its range from 1.61 m to a mere 0.3 m, a loss of no less than 80.8%. And that best range (still assuming the game consists of long jumps across horizontal surfaces) happens with a launch angle of  $30^\circ$ . It lands at a speed no longer equal to launch speed but fully four times slower. (Bos-sard 2002 measured similar launch speeds for cat fleas.)

These insects launch at similar speeds; with smaller size their worlds become draggier and their trajectories less parabolic. Whatever their direction, they jump into the teeth of a sudden, severe windstorm. One has the sense

**Table 1.** Input data and simulation results for the various projectiles. Landing speeds assume launch at the angles that maximize horizontal range and equal launch and landing elevation.

| Projectile           | Effective diameter (mm) | Launch speed ( $\text{m s}^{-1}$ ) | Landing speed ( $\text{m s}^{-1}$ ) | Launch Reynolds number | Best launch angle | Maximum range (m) | Range loss from drag (%) |
|----------------------|-------------------------|------------------------------------|-------------------------------------|------------------------|-------------------|-------------------|--------------------------|
| Cannonball           | 500.0                   | 180.0                              | 155.0                               | 6,000,000              | $43^\circ$        | 3,000.0           | 14.1                     |
| Golf ball            | 42.9                    | 60.0                               | 42.0                                | 170,000                | $41.5^\circ$      | 243.0             | 35.3                     |
| Basketball           | 240.5                   | 20.0                               | 18.0                                | 320,000                | $43.5^\circ$      | 35.7              | 12.3                     |
| Football             | 220.0                   | 30.0                               | 23.0                                | 440,000                | $43^\circ$        | 67.6              | 26.1                     |
| Kangaroo rat         | 100.0                   | 4.4                                | 4.3                                 | 29,000                 | $44.5^\circ$      | 1.84              | 1.1                      |
| Skipper pellet       | 2.8                     | 1.6                                | 1.5                                 | 300                    | $44^\circ$        | 0.246             | 5.4                      |
| Desert locust        | 10.0                    | 3.0                                | 2.8                                 | 2,000                  | $44^\circ$        | 0.85              | 6.1                      |
| Froghopper           | 4.0                     | 4.0                                | 3.0                                 | 1,100                  | $42^\circ$        | 1.22              | 25.0                     |
| Flea beetle          | 1.6                     | 2.93                               | 1.89                                | 310                    | $40^\circ$        | 0.543             | 37.9                     |
| Rabbit flea          | 0.5                     | 4.0                                | 1.0                                 | 130                    | $30^\circ$        | 0.3               | 80.8                     |
| Hura seed            | 16.0                    | 70.0                               | 10.0                                | 75,000                 | $28^\circ$        | 30.0              | 94.0                     |
| Croton seed          | 3.5                     | 8.5                                | 5.6                                 | 2,000                  | $41^\circ$        | 4.6               | 37.5                     |
| Vicia seed           | 2.7                     | 9.0                                | 4.8                                 | 1,600                  | $38^\circ$        | 4.1               | 49.9                     |
| Ruellia seed         | 2.2                     | 12.0                               | 4.7                                 | 1,800                  | $35^\circ$        | 4.9               | 66.5                     |
| Pilobolus sporangium | 0.3                     | 20.0                               | 1.1                                 | 400                    | $17^\circ$        | 0.82              | 98.0                     |
| Sordaria spores      | 0.04                    | 30.0                               | 0.05                                | 80                     | $7^\circ$         | 0.06              | 99.96                    |
| Gibberella spore     | 0.01                    | 35.0                               | 0.003                               | 23                     | $1^\circ$         | 0.0046            | 99.997                   |

that fleas have explored the lower limit of jumping for practical animal locomotion.

## 6. Explosively launched seeds

Plants and fungi may lack equipment for continuous propulsion, but dispersal of their propagules must be as important as is travel for animals. They certainly have ways to give seeds and spores high-speed launches, ways that represent more biological diversity and span a greater range of sizes and initial speeds than in jumping insects. They also make much greater use (with, again, lots of diversity) of elevated launch sites. Still, the same physical imperatives apply. Drag gets relatively worse as size decreases, but so fast are the better among these projectiles that drag can be a major factor even for fairly large ones – much as we saw for golf balls.

Among large ballistic seeds, the current champion appears to be a tropical tree, sometimes planted as an ornamental, *Hura crepitans* (Swaine and Beer 1977; Swaine *et al* 1979). Its disk-shaped seeds (sometimes used as wheels for children's toys) are about 16 mm across and  $350 \text{ kg m}^{-3}$  in density. They launch with quite an audible pop at prodigious speeds, as high as  $70 \text{ m s}^{-1}$  ( $250 \text{ km h}^{-1}$ ). That speed (using horizontal range from ground level as benchmark gets a little artificial for a tree that grows to 60 m) can take them nearly 30 m. Impressive as that distance sounds, it is a small fraction of the 500 m that a *Hura* seed would go in a vacuum – range loss exceeds 94%. Curiously, this fastest speed known in the plant kingdom is indistinguishable from the maximum in the animals, the dive (largely passive and thus comparable) of a falcon (Tucker *et al* 1998).

Smaller seeds that lift off at more modest speeds fall into the same pattern we saw in jumping insects – the smaller the draggier. The 3.5 mm seeds of *Croton capitatus* (Euphorbiaceae), launched at  $8.5 \text{ m s}^{-1}$  ( $30.6 \text{ km h}^{-1}$ ) and  $41^\circ$ , go 4.6 m and pay a drag tax of 37.5%. The 2.7 mm seeds of *Vicia sativa* (Fabaceae), launched at  $9 \text{ m s}^{-1}$  ( $32 \text{ km h}^{-1}$ ) and  $38^\circ$ , go 4.1 m and pay a drag tax of 49.9% (Garrison *et al* 2000). The 2.2 mm seeds of *Ruellia brittoniana* (Acanthaceae), launched at  $12 \text{ m s}^{-1}$  ( $43 \text{ km h}^{-1}$ ) and  $35^\circ$ , go 4.9 m and pay a drag tax of 66.5% (Witztum and Schulgasser 1995).

Explosive seed expulsion occurs less often in still smaller seeds almost certainly because the increased surface-to-volume ratio will result in a further increase in relative drag, whatever the specific aerodynamic regime. Lurking behind the adaptational pattern are the inevitably conflicting demands of ballistic versus wind-borne travel – in effect drag minimization versus drag maximization. For ballistics large size, high density, and compact shape are preferable; for wind carriage small size, low density,

and ramose shapes work better. (Stamp and Lucas 1983, among others, discuss such matters.)

## 7. Explosively launched spores

Small size, though, has proven less discouraging for ballistic spore dispersal by fungi. Most likely, the short stature of most fungi reduces their ability to put spores into the kinds of air movements particularly effective for passive travel. And with truly tiny propagules, even fairly dense spheres will have an agreeably low terminal velocity in free fall, making them better at staying up once aloft.

The most famous fungal projectile is the sporangium of the ascomycete, *Pilobolus*. *Pilobolus* erects its hypha (stalk) a few mm above piles of bovid and equid dung; the sporangium atop the hypha shoots off, with a bit of cell sap, at an initial speed of  $20 \text{ m s}^{-1}$  ( $72 \text{ km h}^{-1}$ ). A sporangium (of the density of water), 0.3 mm in diameter, should go 0.82 m at a best angle of  $17^\circ$ , paying a drag tax of 98%. In fact, sporangia go two or three times that far, almost certainly because they carry that cell sap. It adds mass without much increase in diameter, and it may even provide a slightly streamlined tail. Early in its travel, when going fastest and thus covering most territory, Reynolds numbers of up to 400 are high enough for such shaping to help.

That speed of  $20 \text{ m s}^{-1}$ , incidentally, comes neither from my back-calculation nor stroboscopic measurement. Long ago, A H Reginald Buller (1934) adopted a technique first used (as he says) by Napoleon's technicians when they measured bullet velocities. After firing through two rotating disks of paper they measured the offset of the second hole; that, together with the distance between the disks and their rotation rate, gave bullet speed. Buller used a perforated disk in front and an unperforated one behind, taking advantage of the sporangium's habit of sticking to whatever it hit.

*Pilobolus*, oddly, may make little use of wind. It fires shortly after dawn, not a windy time of day, taking aim at the sun, at that time low in the sky. Perhaps it aims to launch at about that  $17^\circ$  angle that maximizes windless range – no one, I think, has looked into the matter. The objective is a bit of grass or other forage far enough from its own pat of dung to be attractive to another grazer – completion of its life cycle requires passing through a herbivore's gut, and large herbivores (parasite-privy consumers) prefer not to graze too closely to what we used to call horse-apples and cow-pies.

A higher launch speed produces a much lower range in a still smaller projectile. Another ascomycete fungus, one once favoured by geneticists, *Sordaria*, shoots eight-spore clusters, about  $40 \mu\text{m}$  across. Ingold and Hadland (1959) give it a typical range of about 60 mm, from which I cal-

culate an initial speed of  $30 \text{ m s}^{-1}$  ( $108 \text{ km h}^{-1}$ ) and a drag tax of 99.96%. If horizontal range were the objective, its best launch angle would be a mere  $7^\circ$  – in fact, it seems to shoot upward. Why shoot at all? Further above a surface implies greater ambient air movement. With a terminal velocity below  $50 \text{ mm s}^{-1}$ , an upward shot would expose it to moving air for nearly a second, enough time for even the most modest wind to move it laterally.

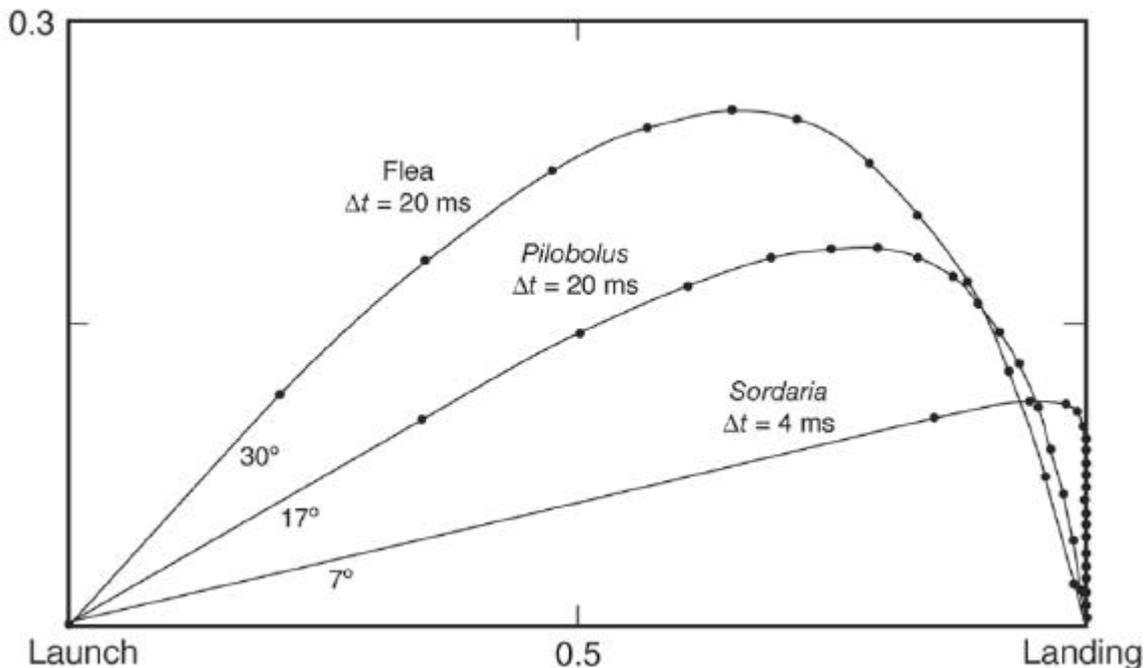
Fungal guns come even smaller. Recently Frances Trail and Iffa Gaffoor measured a range of 4–6 mm for individually ejected ascospores of *Gibberella zeae*, a corn pathogen. Initial speed became important in justifying the high pressure used for launching and in identifying the responsible osmolytes, so I was drawn into the project. From spore density, about that of water, and size, about  $10 \mu\text{m}$ , I calculated the remarkable launch speed of  $35 \text{ m s}^{-1}$  ( $125 \text{ km h}^{-1}$ ). That speed, without drag, would take a spore 125 m, so drag costs it no less than 99.997% of its potential range. It reaches its best range at a  $1^\circ$  launch angle; with a terminal velocity under  $3 \text{ mm s}^{-1}$ , it gets nearly as far (albeit briefly) from the launch site if shot vertically. With a vertical shot from the ground it will be exposed to moving air for about a second and a half and to far longer if launched from the surface of a plant. So that low terminal velocity should not limit its

displacement. Rather, shooting will get it out beyond most or all of the low-speed air near the launch site. At this point, specific data exist for no ballistic projectiles smaller than *Gibberella* spores.

## 8. Generalizing

Why does a higher drag tax inevitably come with a lower optimal launch angle? With greater relative drag, descents are both steeper and slower than ascents. The rule for maximizing range in a draggy world comes down to getting one's distance while one still has decent speed – not wasting that fine launch speed going in a minimally useful direction, in particular, upward. The point becomes clear when one looks at some draggy trajectories that have been marked at uniform time intervals, as in figure 2.

Can aerodynamic lift be used to extend the range of a ballistic projectile? True airfoil-based gliding, used in many lineages of both animals and plants, requires a fairly specialized shape. Another possibility, though, consists of Magnus-effect lift – spinning or tumbling in such a way that the top of the projectile moves in the opposite direction of its overall flight and thus moves with (or at least less rapidly against) the oncoming air. The effect goes by various names in our various sports – slicing,



**Figure 2.** Maximum-range trajectories for three quite drag-afflicted projectiles, a jumping flea, a *Pilobolus* sporangium, and a *Sordaria* eight-spore cluster. Marked points on each curve give distances after equal time increments. Note that axes give horizontal distance as a fraction of maximum range and that the y-axis has been expanded two-fold relative to the x-axis.

top-spin, and so forth; but whatever the name and whether desired or counterproductive, it causes a projectile to deviate from the trajectory that gravity and drag would otherwise determine. But any gain will be small, probably less than 10% in a large seed or jumper and quite a lot less in small forms. Springtails, small flightless insects (order Collembola), appear to use the device (Brackenbury and Hunt 1993), spinning with their upward surfaces moving with the wind at about 16 revolutions per second. Other suggestive cases await investigation.

How might an organism project tiny propagules with less severe limitations than those experienced by *Sordaria* and *Gibberella*? Neither jet nor rocket propulsion occurs in aerial systems, but both the requirement for very high prelaunch accelerations and the disability imposed by drag can be ameliorated. A widely distributed moss, *Sphagnum*, may do so, although I have found no specific investigation of the matter. *Sphagnum* makes a nearly spherical capsule on a stalk well above its green gametophyte body. Prior to launch the walls of the capsule squeeze it down to a more cylindrical form; the increase in air pressure blows off its the lid and the spores go out in the blast of air (Ingold 1939). As a result of that brief tail-wind, they do not immediately encounter the full oncoming wind determined by their speed. And they go off in a cloud-like group. That should permit drag reduction by what in our vehicular world is called 'drafting' and which works far better in the very viscous regime of tiny particles – in effect, pooling mass and reducing effective surface area.

The present essay, like its predecessor (Vogel 2004) and, I hope, its successors, is intentionally eclectic, deliberately bringing together material made heterogenous by our traditional disciplinary divisions. Contriving effective comparisons all too often entails looking at how something performs under circumstances that may be adaptively irrelevant. Thus, as noted, *Pilobolus* may pick a launch angle that gives greatest range; *Sordaria* and *Gibberella* almost certainly do not, with both using ballistics in combination with wind dispersal. Seeds and skipper pellets land at lower heights than those from which they were launched; *Hura* trees, for instance, grow quite tall. So real best ranges and optimal angles require further input data and adjustments of the basic computer program. But beyond exposing underlying commonalities, bringing disparate material together can direct attention to gaps in understanding and to investigational opportunities.

## 9. Predicting and modelling

Finally, we might explore the utility of an index to the degree to which drag will alter (or fail to alter) a ballistic trajectory – a 'range index'. I have found none that gives

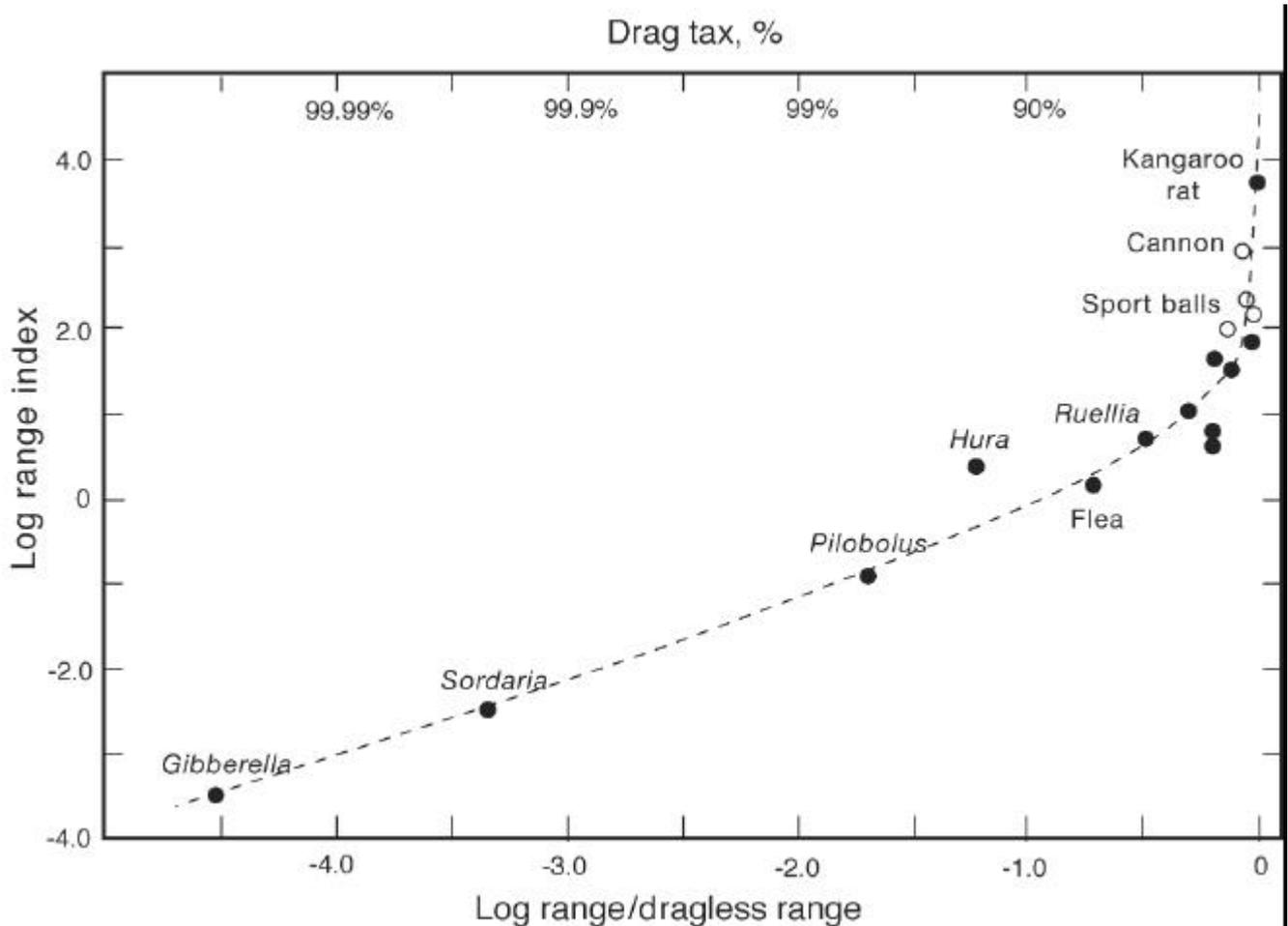
a precise prescription, in part because drag cannot be reduced to a simple proportionality. Still, one can produce an order-of-magnitude index with little difficulty from the ratio of the two forces that contribute to the form of a trajectory, gravity and drag. Gravitational force is proportional to  $mg$  or the product of density, length cubed, and gravitational acceleration. For drag we might use the product of pressure drag and viscous drag. Pressure drag is proportional to the product of density, speed squared, and length squared; viscous drag to the product of viscosity, speed, and length. Squaring gravitational force keeps the index dimensionless; taking the square root of the ratio of gravitational force, squared, to the product of the two forms of drag keeps values from getting unwieldy. Thus we have

$$RI = \left[ \frac{\mathbf{r}_p^2 l_p^3 g^2}{\mathbf{r}_m \boldsymbol{\mu}_m v_o^3} \right]^{1/2} = 2110 \left[ \frac{\mathbf{r}_p^2 l_p^3}{v_o^3} \right]^{1/2}, \quad (7)$$

where subscript  $m$  refers to the medium, air, and subscript  $p$  to the projectile;  $v_o$  is launch speed. The version on the right includes the SI values of gravitational acceleration and the room temperature density and viscosity of air.

This range index suggests two things for biological projectiles, among which density varies by little more than a factor of two. First, high values, meaning minimal effects of drag, will characterize large objects travelling slowly – such as jumping mammals. Conversely, low values, meaning substantial drag effects, will occur with small objects going rapidly. Reynolds number, our usual index for the nature of a flow, includes the product of length and speed; this index uses their ratio. Second, for many fluid problems, what matters is the ratio of viscosity to density, the so-called kinematic viscosity (as in the Reynolds number). Air and water differ only about 15-fold. Here we have the product of viscosity and density; air and water differ by almost 50,000-fold. So shifting to water will cause the index to plunge, and buoyancy will decrease effective  $g$  as well. That rationalizes the scarcity of underwater ballistic devices in either nature or human technology. What about specific values of the index? Figure 3 plots index values for the cases discussed earlier against real range relative to dragless range. One sees that major effects of drag occur when projectiles are very fast (the *Hura* seed) or very small (the three fungal cases), although substantial effects (note the logarithmic scales) happen, as expected, for more ordinary items. Crude as it is, the range index may prove useful in anticipating the performance of yet other biological projectiles without recourse to a recondite computer program.

The range index also serves as a loose rule for making scale models. It enables a person to get a feel, through a



**Figure 3.** The relationship between the range index (equation 7) and real maximum range relative to dragless maximum range (bottom scale) and 'drag tax' (top scale). Open circles are projectiles used by humans.

bit of hands-on activity, for the world of very draggy projectiles. Just weigh a balloon, inflate it, and throw it as far as possible. Estimate launch speed from equation (2) and the range of a thrown projectile of minimal drag. From mass, size, and speed, you can then calculate a trajectory index. For a 150 mm, 0.66 g balloon, I got a value of 0.36, putting it between a jumping flea and a *Pilobolus* sporangium, and suggesting a range loss around 95% – about what happens when I throw the balloon.

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