

Living in a physical world

VI. Gravity and life in the air

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1. Introduction

In our perceptual world, no physical agency imposes itself with greater immediacy than does gravity. We depend on it to walk or run; it injures us if we trip. It makes each of us about half a centimeter shorter at the end of each day than when we first arise. Our flesh sags as we age; more slowly, the glass of a window thickens at the bottom and thins at the top. We dream of escaping its constant crush, although our recent experiences in orbiting spacecraft reveal an addiction with a difficult withdrawal. Physicists may regard the gravitational attraction between two objects as the universe's definitional weak force, but to us large, terrestrial creatures it feels anything but weak.

Since the consequences of gravity depend on one's size, scaling will loom at least as large in this and then the next as in any of the preceding essays. Even more important than the ways gravity's effects, scale will be another message—the surprisingly wide range of biological situations in which it plays some role. One knows that no massless world exists; I would argue that a weightless world is almost as hard to imagine.

That contrast, mass versus weight, needs a few words. Newtonian mechanics lumped two distinct kinds of mass, inertial mass and gravitational mass. Establishing the basis of their apparent equality awaited the 20th century. An inertial mass resists acceleration, as expressed in Newton's first and second laws; quantitatively, mass equals force divided by acceleration—the familiar $F = ma$. Weight follows from the other kind of mass. A gravitational mass attracts any other mass, exerting a force equal to the product of the two masses, divided by the square of the distance between them, times a universal gravitational constant, in proper SI units, $6.67 \times 10^{-11} \text{ N m}^2 \text{ kg}^{-2}$. (One should avoid using “gravitational constant” for the acceleration of gravity at the surface

of the earth, commonly designated g .) In our world that other mass is that of the earth itself, $5.976 \times 10^{24} \text{ kg}$, and the basic distance is that from the earth's surface to its center of mass, 6,370 km. These data give $g = 9.8 \text{ m s}^{-2}$; with $F = mg$ we can then convert mass (kilograms) to terrestrial weight (newtons).

Our lack of intuitive feeling for the difference between mass and weight just reflects inexperience with situations in which the constant of proportionality differs from the terrestrial 9.8 m s^{-2} or, because of our buoyancy, an effective value near zero when submerged. Think back to video images of astronauts ambulating on the surface of the moon. Unsurprisingly, they adopted a rather bouncy gait when going straight ahead; one could easily fail to notice the greater forward tilt needed to get going. Turning, though, looked glaringly unfamiliar with a greater lean needed to change direction. Greater tilts to start, stop, and turn provided sufficient force so these weight-deprived individuals could accelerate their unchanged masses, to apply what weight they retained with sufficient effect. Fortunately, the human neuromuscular machine turns out to cope remarkably well with this completely novel six-fold reduction in weight.

2. The other forces that matter

Besides that of gravity, life contends with a diversity of forces—for instance that inertial force from the unwillingness of mass to accelerate; the force of surface tension from the cohesion of liquids in gases or in other, immiscible, liquids; and viscous force from the resistance of both liquids and gases to shearing motion. In most situations, though, we only need worry about one or two forces, and the first item in an analysis commonly consists of identifying the forces at work and their relative importance. An extreme example should emphasize the point.

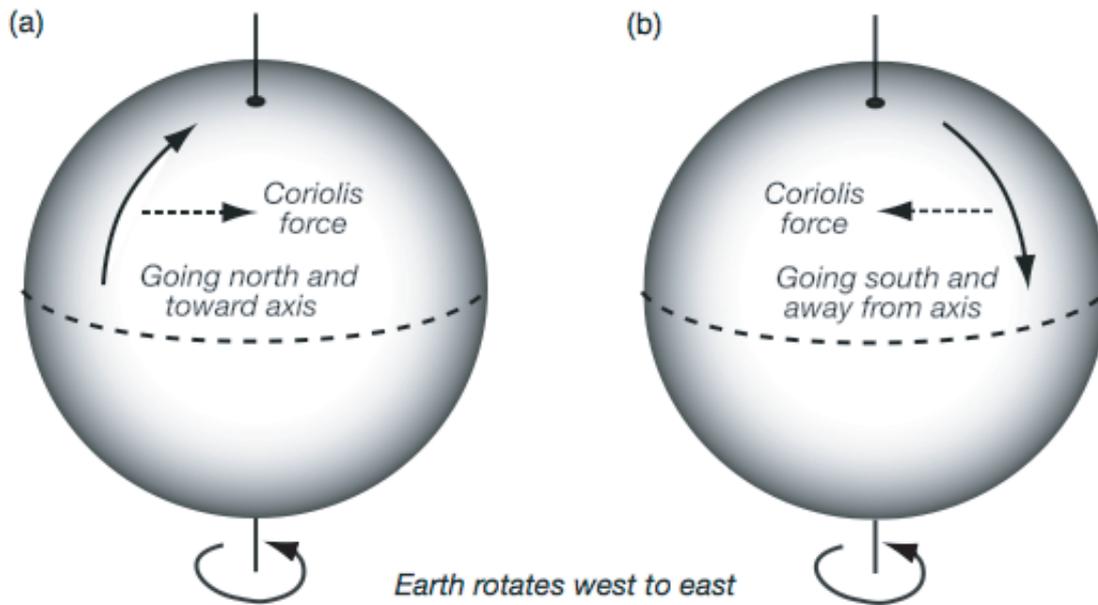


Figure 1. The origin of the Coriolis force for something moving (a) northward and (b) southward, in the northern hemisphere. While the force may be eastward and then westward relative to the earth, it remains to the right with respect to the mover.

Some time ago, I was asked to evaluate a claim that the asymmetries of the mammalian body, in particular of our own, could be traced to effects of the Coriolis force from the earth's rotation on the evolution of terrestrial animals. That force (really a pseudoforce, like so-called centrifugal force) results from the spherical rather than cylindrical shape of the rotating earth. Thus (as in figure 1) an object in the northern hemisphere moving north must move inward toward the earth's axis of rotation as well. Angular momentum being conserved, it should rotate faster—the effect will be felt as an eastward force, a force to the right of its path. When moving south, the object will move outward and thus try to rotate more slowly—an effect now felt as a westward force, but still to the right of its path. Clearly a slightly sturdier right leg ought to confer an advantage, making an animal, one might say, a leg up. The same argument was applied most ingeniously to our many anatomical asymmetries.

I found against the plaintiff, so to speak, making my case by comparing the magnitude of the Coriolis force with that of the gravitational force. The former is twice the product of the object's mass (m), the speed at which it moves north or south (v), the earth's angular velocity (Ω), and the sine of the latitude (ϑ). Mass times gravitational acceleration (mg) gives the gravitational force. In their ratio, mass cancels, and we get

$$\frac{2v \cdot \Omega \cdot \sin \vartheta}{g} \quad (1)$$

A most-favourable-possible-scenario might consider an animal living at 45° latitude and spending its life going north or south at 1 m s^{-1} . Under these conditions the ratio is 1:100,000. That seemed to me to offer evolution precious little advantage with which to work; for more evolutionarily reasonable lower speeds and latitudes, the ratio would be still less auspicious. In short, little about our persons can be attributed the Coriolis force—however dramatic its effects on, for instance, weather patterns.

[As noted by a reader of the manuscript, the equation should not be applied in this simple form to the large bodies of air responsible for our weather. It ignores buoyancy, tacitly assuming that the density of the mass at issue far exceeds that of the atmosphere. Persson (1998) provides an engaging introduction to Gaspard Gustave de Coriolis (1792–1843) and his force.]

While the terrestrial Coriolis force may be summarily dismissed relative to gravity, many other forces cannot. Hydrostatic and aerostatic forces squeeze or expand organisms. Tensile, compressive, and shearing forces variously distort their shapes. The viscosity and dynamic pressures of flows impose both drag and lift. The inertia of fluids can exert major transient forces, as when the surface of a body of water is slapped—by a hand or, more significantly, when a basilisk lizard runs across a stream (Glasheen and McMahon 1996). Transpiring trees as well as water striders depend on surface tension. And so on. What most often

determines the practical consequences of gravity is its magnitude relative to the other forces at work.

The engineering community, the fluid mechanists in particular, have long used a variety of dimensionless ratios of one force to another to evaluate their relative importance. Gravitational force contributes to many of them, either as numerator or denominator depending on the prejudice of the particular field in which the ratio first found use—which force carried the load and which constituted a nuisance. For instance, the Bond number, below, has mainly been used for gravity-driven flows with interfaces in porous media, so gravity makes the system go, while surface tension acts as a brake. Thus using gravitational force as numerator and surface tension as denominator makes high rather than low values desirable. If, instead, the ratio had been contrived by a biologist concerned with animals supported by surface tension atop a pond, gravitational force would have dropped to the denominator.

Among the dimensionless ratios that include gravitational force (from Weast *et al* 1987; new editions of the *Handbook of Chemistry and Physics* no longer give dimensionless ratios)....

(i) Bond number—as mentioned, gravitational force to surface tension force:

$$Bo = \frac{(\rho_o - \rho_m)l^2 g}{\gamma} \quad (2)$$

ρ_o and ρ_m are the densities of object and liquid medium respectively, l is a characteristic length of the system, the choice depending on the particular phenomenon at hand, and γ is surface tension.

(ii) Froude number—inertial force to gravitational force:

$$Fr = \frac{v^2}{gl} \quad (3)$$

The choice of l , again, depends on the system.

(iii) Bagnold number—drag to gravitational force:

$$Ba = \frac{3C_d \rho_m v^2}{4d \rho_o g} \quad (4)$$

C_d is the object's drag coefficient and d its diameter. It resembles the Froude number because the underlying formula for drag ($1/2 C_d \rho_m S v^2$, with S for projecting area normal to flow, as in eq. 12, below) tacitly presumes it an inertial force and ignores buoyancy by assuming an object much denser than the medium.

(iv) Grashof number—buoyant force to viscous force:

$$Gr = \frac{\rho^2 g \beta (\Delta T) l^3}{\mu^2} \quad (5)$$

β is the coefficient of thermal expansion of the fluid, ΔT the temperature difference, and μ the viscosity. The Grashof number appeared previously in essay 4 (Vogel 2005b).

(v) Galileo number—gravitational force to viscous force:

$$Ga = \frac{l^3 g \rho^2}{\mu^2} \quad (6)$$

Since gravity underlies buoyancy, similarity between this one and its predecessor should be no surprise. Both the Grashof and Galileo numbers, as well as a few others, include as a factor the Reynolds number,

$$Re = \frac{\rho l v}{\mu} \quad (7)$$

the ratio of inertial to viscous force—thus density and viscosity appear as second powers in both.

In all these dimensionless numbers (as well as others), the larger the system, the more important gravity becomes relative to other forces. Whether g appears as numerator or denominator, some size factor appears with it. I can think of no exception to that rule, although I hesitate to assert its universality.

3. Going up and down

Besides keeping our atmosphere from drifting away, gravity makes its outer portions squeeze down on the inner portions; thus a pressure increase accompanies an approach to the earth's surface. (Only a tiny part of that increase comes from the increase in gravitational force as the earth's center is approached.) As in any ordinary gas mixture, atmospheric density follows pressure—some consequences of altitude change result from density change, others from pressure change. In particular, pressure affects the solubility of gases in liquids. A carrier of respiratory gas such as haemoglobin, suitable for reversible binding with oxygen at one altitude, will not work as well at a very different one, and mammals adapted by ancestry (as opposed to individual experience) to high altitudes have haemoglobin variants with greater affinities for oxygen (Hall *et al* 1936).

The volume of a helium- or hydrogen-filled balloon will increase as it rises; if its buoyancy varies with volume and its drag with surface area, its ascent speed will gradually increase. Organisms, though, do not use buoyant bags to ascend in air. Still, the volume increase does matter, requiring that internal air containers either be surrounded by stretchy walls or be vented to the outside. We vent our middle ears into our respiratory passages through a pair of Eustachian tubes, and ascents and descents in aircraft or elevators with plugged tubes cause pain and temporary auditory impairment. Birds, facing the problem in more severe form, vent all their air-filled bones.

The external effects of that volume increase with altitude (or with anything else that lowers pressure) may be more important. If a patch of ground heats more than the surrounding area, the locally warmer air above it may rise. It initially forms a column, then a round bubble, and finally a torus. That rising torus, typically over a highway or plowed field, can provide an elevator for pollen, spores, seeds, and small organisms.

One might expect that any ascent will be brief, since such objects will always be descending relative to the local air and must soon fall out of the ascending torus. That need not be the case – the torus forms because air at the periphery of the bubble is slowed by the surrounding air. Thus air near the periphery descends relative to the overall structure, and air near the inner portion of the ring must rise. So something near the inside margin of the toroidal ring can fall steadily without falling out. Many birds appear to do just that, soaring in circles whose radii are smaller than the radii of the cores of the tori. That need to glide in fairly tight circles has been invoked to explain the typically short and broad wings of terrestrial – by contrast with marine – soarers. Other creatures, such as tiny spiders and insects may exploit the same opportunity by paying out long threads that partly enwrap vortices, although we lack specific documentation.

Locally warmed air rises; locally cooled air should fall. Such cold, downslope currents, mainly at night, often occur in hilly or mountainous terrain. Extreme versions go by names such as “air avalanches,” ‘mistrals’ and ‘williwaws’ and may reach 40 m s^{-1} ; Geiger (1965) describes ones of remarkably regular short-term periodicity.

Large scale mixing may not always suffice to keep the atmosphere uniform, and the resulting local changes in atmospheric composition can have serious physical and biological consequences. Local enrichment with a light gas such as methane will produce upward bubbles, columns, and toroids just as does local heating, if on a smaller scale and less portentously. Local enrichment with a heavy gas will, in the absence of significant wind, lead to a stable, enriched layer at ground level. A ground-level layer of carbon dioxide, not normally regarded as a serious toxin, led to the Lake Nyos disaster of 1986 in West Africa (Kling *et al* 1987). After the outgassing that began at some supersaturated spot deep within the lake, CO_2 reached sufficient concentration to cause the immediate death of the 1700 or so people of the surrounding villages.

4. Falling in air

When acting directly on the mass of an organism, gravity has consequences both more common and serious than anything resulting from changes in atmospheric pressure and density. Unrestrained, a body accelerates downward

at 9.8 m s^{-2} , so

$$v = \sqrt{19.6d}. \quad (8)$$

The impact speed after a fall of a meter will be 4.4 m s^{-1} , tolerable for most organisms under most circumstances. A 10 m fall will give an impact speed of 14 m s^{-1} and a 100m fall of 44 m s^{-1} , both ordinarily hazardous.

In reality, a body falling in air accelerates ever more gently, asymptotically approaching a state where its downward gravitational force equals its upward drag, where the Bagnold number (above) approaches 1.0. The apparent calculational simplicity, though, proves deceptive. As noted when considering trajectories in essay 2 (Vogel 2005a), C_d , the drag coefficient, varies peculiarly. For very small things falling in air – fog droplets, pollen grains, and so forth – it varies inversely with speed (more specifically, with the Reynolds number and as described by Stokes’ law), while for large, fast, dense things it remains very nearly constant. In between, from ejected spore clusters, falling seeds, and small, flying insects to medium-sized flying birds – no biologically trivial realm – we find several shape and Reynolds-number dependent transitions, some of them abrupt (Vogel 1994).

Figure 2 gives terminal speeds for spheres of the density of water falling in air of sea-level density, calculated using the formulas of essay 2. (Streamlined bodies, at least ones of large or moderate size, will reach higher terminal speeds, while irregularly shaped or tumbling bodies will descend more slowly.) Bigger inevitably means faster, but for small spheres terminal speed is especially size-dependent, increasing with the square of diameter according to Stokes’ law, while for large ones terminal speed increases with only the square root of diameter.

Still, one should not assume that drag must always be taken into account. In figure 3 the same equations have been used to view the approach to terminal speed for spheres of a range of sizes (again at one atmosphere and of water’s density). For large bodies, long drops precede achievement of near-terminal speeds, while small ones get there so shortly after release that one can assume they accelerate instantaneously. For instance, to get within 5% of terminal speed, a 100 mm sphere needs about 100,000 mm of fall; a 10 mm sphere needs about 2,000 mm of fall; a 1 mm sphere needs about 100 mm of fall; a 0.1 mm sphere needs about 0.1 mm of fall; a $10 \mu\text{m}$ sphere needs a mere $0.01 \mu\text{m}$ of fall. A 10^4 -fold decrease in diameter yields a 10^{10} -fold decrease in the dropping distance to get to 95% of terminal speed.

Alternatively, one can view (as in figure 3) the scaling in terms of the diameters of the spheres, using falling distance over diameter as a nicely dimensionless length. To get to our benchmark 95% of terminal speed, the 100 mm sphere takes 1000 diameters, the 10 mm sphere takes 200 diameters, the 1 mm sphere takes 100 diameters, the 0.1 mm

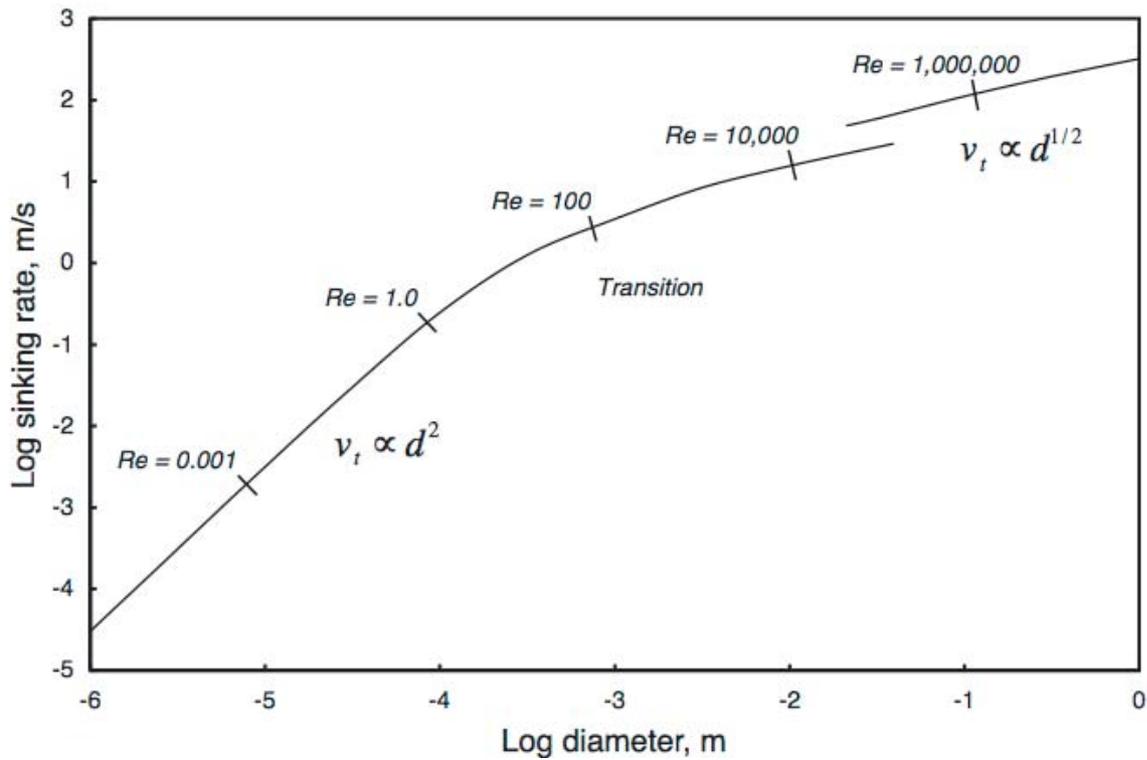


Figure 2. Terminal sinking rates of spheres without induced internal motion and of the density of water as a discontinuous function of diameter and Reynolds number (eq. 7, using the density and viscosity of air).

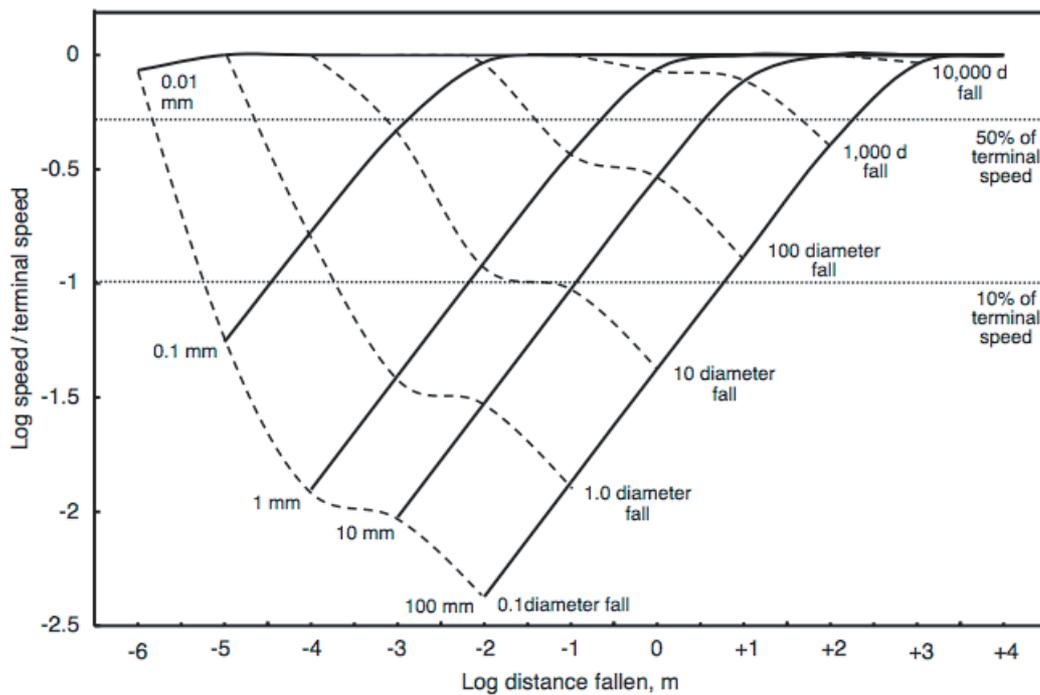


Figure 3. How the approach to terminal velocity varies with the size of spheres of density 1000 kg m^{-3} falling in air.

sphere takes 1 diameter, while the 10 μm sphere takes a mere 0.001 diameter. (The peculiarly irregular variation of drag with speed for falling spheres and most other ordinary shapes makes the sequence somewhat erratic.)

In short, when falling in air, drag and terminal speed carry biological significance mainly for small objects— unless, of course, one considers selectively questionable behaviour such as sky-diving by humans. Still, even small ones may run out of range of Stokes' law, reliable only for Reynolds numbers decently below 1.0, so one may need to do calculations such as those that generated figures 2 and 3. A sphere 1 mm in diameter will exceed $Re = 1.0$ after a fall of less than a millimeter, long before reaching terminal speed (at which $Re = 230$), indeed well before drag has begun to alter its motion much at all. Even a 0.1 mm sphere, about at our visual threshold, will exceed $Re = 1.0$ at terminal speed.

What happens below diameters of about 10 μm ? Stokes' law gives unambiguous results with no uncertain coefficients. Unfortunately an exceedingly basic assumption, one only infrequently made explicit, begins to break down and restrict its reliability. For the most part, fluid mechanics treats fluids as continua—non-particulate, infinitely divisible without loss of character. While 10 μm remains far above molecular dimensions, molecular phenomena nonetheless start to intrude. The terminal speeds of particles begin to deviate from those anticipated by Stokes' law as their diameters approach the mean free paths of the molecules of their surrounding fluid. For air, mean free paths are of the order of 0.1 μm , only two orders of magnitude smaller than the 10 μm spheres considered here and closer still to, for instance, a 4- μm spore of the fungus *Lycoperdon* (Ingold 1971).

In effect, the Brownian motion due to random collisions with moving gas molecules rises to the same scale as that caused by gravity, so motions become irregular, eventually having only a statistically-downward bias. The relative magnitude of the effect increases rapidly with decreasing particle size both because gravitationally-driven descent speed decreases and because the effective Brownian displacement speed increases. (The later, as noted in the first of these essays is a peculiarly duration-dependent speed, here the square root of the quotient of twice the diffusion coefficient for a particle of a particular size divided by a reference time.) For a 10 μm particle (still of water's density sinking through air) and a reference time of 1 s, Brownian displacement speed is less than a thousandth of gravitational speed; for a 1 μm particle (perhaps an airborne bacterium), Brownian displacement speed rises to a fifth of gravitational speed; for a 0.1 μm particle, Brownian speed approaches a hundred times gravitational speed (Monteith and Unsworth 1990; Denny 1993).

Further clouds on the horizon need more mention than they usually get, suggesting caution in adopting textbook equations. The equations that generated figure 3 assume quasi-steady motion in an unbounded fluid; that is, they take no account of any special phenomena associated with

acceleration. At least two unsteady phenomena can take on importance, one largely independent of the fluid's viscosity, the other its direct consequence.

First, when a body accelerates in one direction, fluid must accelerate in the other. The latter requires force no less than the former; it goes as the "acceleration reaction force" or simply the "acceleration reaction". For a sphere, one calculates the extra force by presuming that the body has an additional mass equal to half that of the volume of fluid it displaces—that half is the "added mass coefficient" of a sphere (Daniel 1984, Denny 1988). So accelerations are less than calculated for a quasi-steady case—as if drag were increased, but with the effect scaling with volume rather than diameter or cross section. Decelerations are also reduced, with the acceleration reaction now opposing drag. For a sphere of biologically relevant density in air, the acceleration reaction will usually be negligible next to drag. It should matter, though, for a buoyant balloon just after release. In water, the acceleration reaction can be a major factor. In at least one circumstance it dominates—for the initial ascent of a bubble of gas in a liquid. Here the mass, even half the mass, of the displaced fluid far exceeds that mass of the accelerating body, so neglecting the acceleration reaction gives an acceleration overestimate of several orders of magnitude (Birkhoff 1960).

Second, setting up a steady-state flow pattern around a body takes time, so a history term may be significant during acceleration. Again, accelerations are reduced, here because velocity gradients and thus shear forces are more severe than otherwise expected. Again, the effect, often called the "Bassett term," (Michaelides 1997; Koehl *et al* 2003) will only rarely be important for ordinary bodies accelerating in air.

[The Bassett term is analogous to the long-known Wagner effect (Wagner 1925; Dudley 2000), a delay in the development of aerodynamic lift as an airfoil begins to move. Moving those initial 7 or 8 wing widths cannot greatly tax the run-up to take-off of an airplane; but it demands special devices for animals that, lacking rotational propellers, must flap their wings, starting each wing twice during each stroke.]

Nor do the usual equations worry about wall effects or interparticle interactions, which occur whether a body is accelerating or moving steadily. They result mainly from viscosity and the resulting velocity gradients. A body falling near a wall falls more slowly, sometimes much more slowly; the lower the Reynolds number, the more severe the effect and the more distant can be a confounding wall. And one starting from a surface will have a lower initial acceleration. Conversely, a body falling in the wake of another will experience lower drag and tend to catch up; a cloud of tiny bodies can thus coalesce as the bodies fall. These effects are more likely to be more important in air than are the acceleration reaction and the Bassett term, at the same time they

are easier to identify and avoid. Not that biologists do so consistently—a substantial literature for sinking rates in nature comes from measurements of the descent speeds of clouds of individuals in worryingly narrow tubes.

5. Another way to descend slowly

The higher a body's drag, the slower gravity will make it descend, at least, when drag has acted for a sufficient time. Alternatively, descents can also be slowed with some kind of lift-generating airfoil—a device that produces a force component at right angles to the oncoming airflow as well as the inescapable drag, parallel to flow. Not only does this mode of descent-slowness have quite a different aerodynamic basis, but it imposes an antithetical requirement. The effectiveness of a lift-producing airfoil depends on its lift-to-drag ratio. That implies minimization rather than maximization of drag.

Higher Reynolds numbers allow airfoils to achieve greater lift-to-drag ratios, so using lift to slow descents becomes increasingly attractive as systems enlarge. Thus airborne seeds (or fruits or seed-leaves—more generally, 'diaspores' or 'propagules') that slow descents by increasing drag mostly have masses below 50 to 100 mg; very few of what Augspurger (1986) terms 'floaters' exceed that benchmark. Ones heavier than this, such as the samaras of maples, ashes, and tulip poplars, mostly employ lift-producing airfoils; conversely samaras come no lighter than about 10 mg (Azuma 1992). By contrast, animals such as flying squirrels that can control their aerial postures blur the boundary, with no hard and fast distinction between drag-based parachuting and lift-based gliding—more about these shortly.

What the lift-to-drag ratio sets is the angle with which a gliding airfoil descends, whether a glider moves in one direction or, as does a samara, takes a helical path as it autogyrates downward. Specifically, the lift-to-drag ratio, L/D , (for the entire craft if made of more than a single airfoil) equals the cotangent of the angle relative to the horizontal, ϵ , of a steady-speed descent:

$$\frac{L}{D} = \cot \epsilon \text{ and } \frac{D}{L} = \tan \epsilon. \quad (9)$$

But although it sets the path, the ratio does not fully determine the speed at which the craft approaches the earth. For a steady glide, descent speed depends as much on the amount of upward force needed, which must equal the weight of the craft. Since lift (like drag) is proportional (putting aside some secondary matters) to the square of speed, that square of speed varies directly with weight. Doubling the weight of a glider increases its steady-state speed (both overall and descent speeds) by 1.414. Thus in still air (and

assuming a unidirectional glide, not an autogyrating vertical descent), the heavier glider will go about as far when released from a given height, but it will get there faster.

That independence of glide angle and weight may underlie the large size of some fossil fliers, whether insects (Paleodictyoptera) or reptiles (pterosaurs). One hastens to add at least one caution, though. One might imagine that, assuming biologically-ordinary tissue densities, an increase in the weight of a glider will be offset by the increase in wing area and thus lift, which varies direct with it. But the scaling of wing area and body mass, about which more in the next section, undercuts that offset. For isometric craft of constant density, lift will vary with wing area, S , and thus body area and length squared, while weight will vary with length cubed, so

$$W/S \propto l. \quad (10)$$

That variable, W/S , goes by the name "wing loading." As a consequence of its scaling with length, bigger must mean faster, at least if size increases isometrically. That demands some combination of shorter glides, more wind-dependent take-offs, and harder landings. Perhaps those large fossils tell us that back when few fast terrestrial predators lurked, isometry could be put aside—the increased fragility of light construction and disproportionately large wings may have been less disadvantageous.

(Wing loading may enjoy a weight of tradition, but it ignores at least one potentially confounding factor. Long, narrow wings do better than short, wide ones, something now well understood, but evident only empirically in the early days of flight. To avoid giving equal weight to length and width in wing area, an alternative variable, "span loading", the ratio of weight to the square of the wing span, sometime finds use. Choice of variables matters little for wings of ordinary proportions or for comparisons among wings of similar shapes.)

So both glide angle and wing loading (the relevant form of weight) enter the picture. The first looks at first glance as if size-independent, while the second is inimical to large craft. In addition, there is a third variable, one inimical to small craft. Lift, or properly the lift coefficient (C_l) of a high-quality airfoil, depends only slightly on Reynolds number, at least for Re 's above those of fruit-flies, around 100; it usually has a value of about 1.0 or a bit less at a maximal lift-to-drag ratio. By contrast, drag, expressed as the analogous drag coefficient (C_d), drops with increases in the Reynolds number. Formally defining those coefficients, we have

$$L = C_l \rho_m v^2 S / 2 \text{ and} \quad (11)$$

$$D = C_d \rho_m v^2 S / 2, \quad (12)$$

where ρ_m is the density of the medium and S is the projecting area, normal to flow, of the airfoil. In effect, the best achievable lift-to-drag ratio will increase (if complexly)

with size, putting small gliders at a disadvantage when it comes to glide angle.

How much so? Looking at how a specific airfoil's or aircraft's performance varies with Reynolds number will most likely mislead us, since effective airfoil design itself varies with Re . So we might compare a heterogeneous collection, ones that have proven effective under their individual operating conditions. Figure 4 gathers data for lift-to-drag ratios for airfoils as a function of Reynolds number; these, bear in mind, are data from diverse sources with embedded estimates to render them commensurate. A competitive sailplane may have a ratio of 50; a top-flight bird, an albatross, of 20; the hindwing of a desert locust about 8; flies and bees around 2; test airfoils at $Re = 10$ and $Re = 1$ of 0.43 and 0.18 respectively. Clearly small fliers cannot achieve glide angles as low as those of large fliers, and the increasing glide angles at Reynolds numbers below about 500 make gliding itself impractical. Some large insects glide, at least occasionally; small ones do not.

In one sense, though, the inferior glide angles of insects (and, although less extreme, of birds) may mislead us. In

that earlier assertion that as wing loading went up with body size so must flying speed lies a compensating advantage of small, if not very small, size. In the real world, gliding in a temporally and spatially uniform atmosphere represents both a worst and an uncommon case. We know quite a few ways gliders can take advantage of atmospheric structure, what we have taken to call 'soaring' as opposed to simple gliding. Most schemes for soaring depend as much or more on time aloft than on the horizontality of simple gliding. Time aloft, of course, varies inversely with sinking speed, so time aloft is no worse for a flier that descends twice as steeply if it flies half as fast. With still-air time aloft as the criterion, gliding/soaring retains utility down into the large insect range—it may even improve. A limit line drawn through the upper left set of points in figure 4 has a slope of 0.217. Converting from lift-to-drag ratio to sinking speed tells us the latter will vary with $Re^{0.116}$ for isometric gliders of equal lift coefficients (eq. 11). So the smaller glider will approach the earth somewhat less rapidly in still air or, of more relevance, slower ascending air will suffice to keep it aloft. Tucker and Parrott (1970) make just this point,

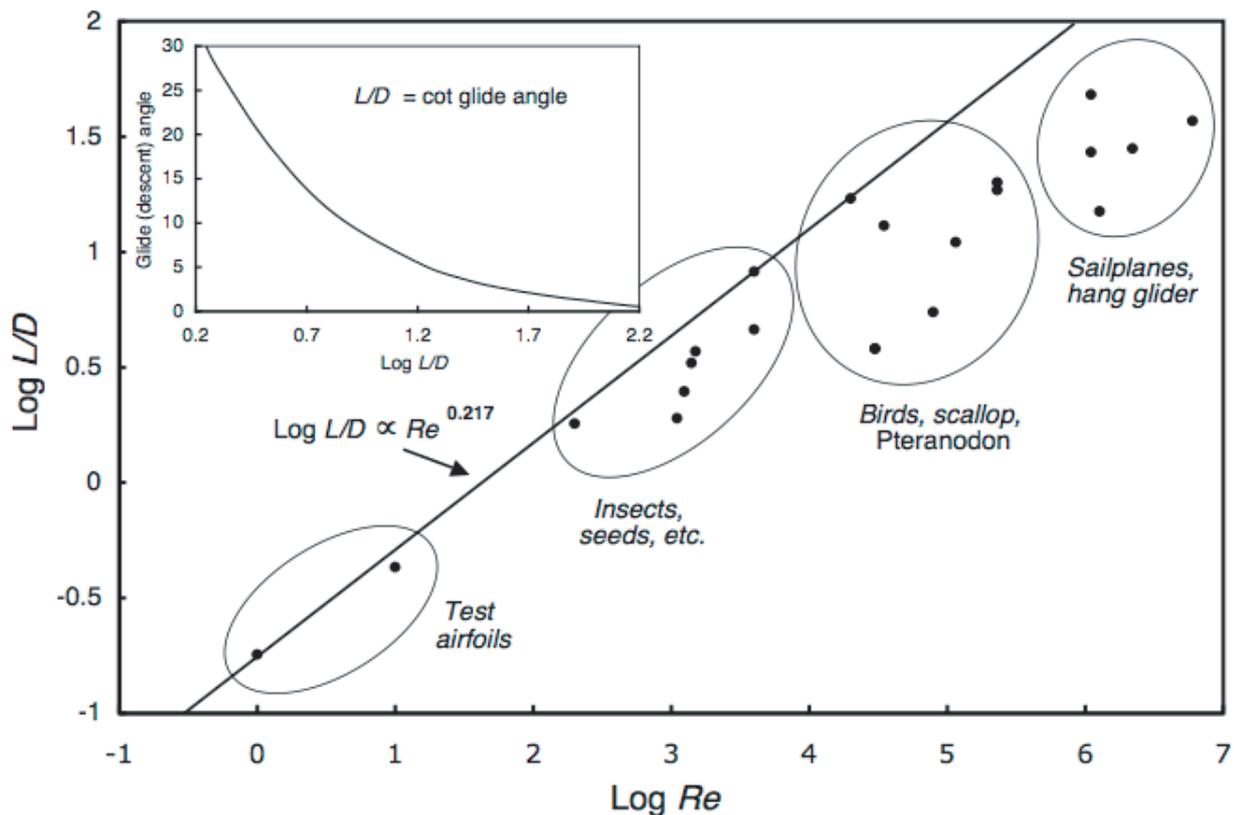


Figure 4. The scaling of the lift-to-drag ratio with Reynolds number, with an empirical limit line. The inset provides a conversion of the ratio to the steady-state glide angle with respect to the horizontal. Data for human-carrying craft from commercial websites; *Pteranodon* from Bramwell (1971); scallop from Hayami (1981); birds from Withers (1981); insects from sources in Vogel (1994, p 249); seeds from Azuma (1992); test airfoils from Thom and Swart (1940).

noting that soaring birds such as some vultures can achieve lower minimum sinking speeds than high-performance sailplanes.

So why do not tiny, even microscopic, gliders fill the skies? Flapping fliers blur the issue, with what appears to be a gradual diminution with decreasing size of the extent to which they employ intermittent gliding; locusts, butterflies and dragonflies glide at least a little; bees and flies do not. Purely passive gliders provide a clearer dichotomy. Among plants—those wind-dispersed, autogyrating samaras, mainly—as noted earlier, gliders get no smaller than about 10 mg and fly at Reynolds numbers no lower than about 500. Among animals, purely passive gliders drop out below about 1 g (McGuire and Dudley 2005). That initially puzzling 2-order-of-magnitude difference may just be a matter of adaptational opportunities or lack of alternatives such as active flight. Still, the absence of a fauna analogous to the samaras seems odd. Arboreal insects have the option of flight, but where are the gliding arboreal spiders?

The data collected in figure 5 may provide a bit of insight. Perhaps that slight improvement with decreasing size eventually competes with an alternative that offers still

better scaling. The left, linear portion of figure 2 implies that sinking speed for objects retarded by drag will vary with $Re^{0.67}$, more drastic than the $Re^{0.116}$ for lift-based retardation, an implication well confirmed by the real-world data of figure 5. Smaller becomes not a bit but a lot better than for craft that slow their descents by maximizing drag. Blurring the contrast just a little, the drag-based floaters, while generally lighter than the lifters, operate in a realm with an intermediate scaling exponent—with sinking speed proportional to $Re^{0.33}$ as on the right side of figure 2. And without obvious exception, they keep sinking rates reasonable through drastic surface proliferation, equipping themselves with all manner of hairs, fluff and appendages.

Too quick a look at such data for both glide angle and sinking speed may mislead us in another way. It accords poorly with the repeated evolution of remarkably bad gliders in several groups of terrestrial vertebrates—frogs that glide using oversize webbed feet, lizards that glide with lateral trunk extensions, squirrels and phalangers that glide with thin skin that stretches from fore to hind legs, even snakes that glide with a bit of body flattening and a

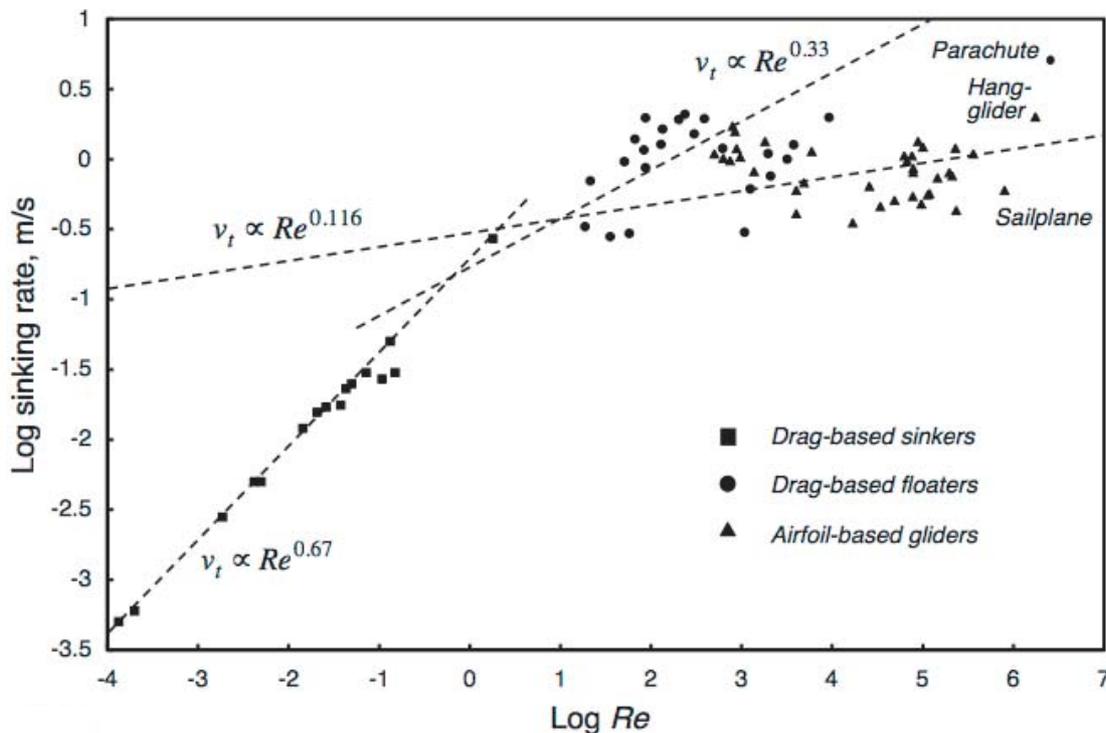


Figure 5. Sinking rates of passively sinking or gliding systems spanning an especially wide size range and anything but isometric. Note that while the exponents of the scaling lines can be justified, their positions are arbitrary. The exponent of 0.116 comes from the empirical limit line of figure 4; the exponents of 0.33 and 0.67 are theoretical and come from figure 2. Sources: Azuma (1992), Bramwell (1971), Gibo and Pallett (1979), Ingold (1971), Jensen (1956), McGahan (1973), Niklas (1984), Okubo and Levins (1989), Parrott (1970), Pennycuik (1960, 1971, 1982), Rabinowitz and Rapp (1981), Tennekes (1996), Trail *et al* (2005), Tucker and Heine (1990), Tucker and Parrott (1970), Verkaar *et al* (1983), Ward-Smith (1984), Werner and Platt (1976), and Yarwood and Hazen (1942).

cross-flow body orientation (see, for instance, Dudley and DeVries 1990; Norberg 1990). None of these achieves an especially high lift-to-drag ratio for its size; values run from a little over 2 to a little under 5 (Socha 2002). The apparent paradox may stem from the way both glide angle and descent speed tacitly assume steady-state activities. These may be the exception rather than the norm in these animals—why I omitted them from figure 5. A large part of a trajectory typically consists of an initial outward and then downward leap, with only a minor aerodynamic component; the path then becomes ever less vertical. Major and deliberate drag increases may precede landings, raising lift at the expense of speed and the lift-to-drag ratio, in a sense reinvesting the momentum of the initial leap when airspeed is no longer an asset.

Recent work on flying snakes, genus *Chrysopelea*, (Socha *et al* 2005; see also www.flyingsnake.org) and on lizards, genus *Draco* (McGuire and Dudley 2005) provide object lessons. Clearly the old and often quoted distinction between parachuting and gliding, whether the trajectory descends more or less steeply than 45°, is worse than arbitrary; its implied scenario diverges misleadingly from reality.

One point of figure 5, the superiority making lift rather than drag for staying aloft—at least for Reynolds numbers high enough for decent lift-to-drag ratios—can be argued in another way. Consider a hypothetical drag-based descender that loses altitude at the same rate (0.41 m/s) as the winged seed-leaf of the Javanese cucumber *Alsomitra* (*Zanonia*), which operates at $Re = 4000$ (Azuma and Okuno 1987; Alexander 2002). If the descender weighed no more than that seed-leaf (210 mg) and took the form of a flat horizontal disk (thus normal to the upward relative flow: $C_d = 1.2$), it would need an area of 3.4 times that of *Alsomitra*'s 0.005 m². And the latter operates at the unimpressive lift-to-drag ratio of 3.7, apparently accepting a lesser value than its best 4.6 to gain the intrinsic stability critical for a totally passive glider. For a similar reason, windmills with blades rotating in a plane normal to flow became common and displaced ones turning horizontally, like cup anemometers, about a thousand years ago. Ships with propellers displaced most drag-based side-wheel and stern-wheel boats, starting a century and a half ago. Both transitions preceded the aircraft-stimulated development of propellers that could achieve respectable L/D ratios.

The dichotomy between drag-based and lift-based descent-slows carries a further message. That size-dependent shift from drag as good to drag as evil may constitute an odd adaptive barrier—a device well-attuned to one mode will ordinarily be especially bad in the other. Active flight has evolved from gliding flight whenever it has appeared, but gliding flight seems never to have evolved from drag-based descent retardation. One serious suggestion that flying insects took that route (Wigglesworth 1963) has never

gained substantial support. The nearest thing to an evolutionary switch I can think of occurs in a few Lepidoptera such as the gypsy moth (*Lymantria dispar*), a notorious pest in North America. Instead of basing dispersal on actively flying adults, the first instar caterpillar does the job by paying out long silk strands as if a newly-hatched spider.

Not that one cannot imagine plausible designs that might permit fairly easy shifts from, say, drag maximization to gliding in passive craft. A round horizontal disk with a mass on a rigid stalk beneath its center will descend with lots of drag. Moving the stalk and mass closer to an edge could convert the device to something like a hang-glider, with better still-air dispersal distance as a selective reward. I would not place a bet, even at good odds, against the reality of such a scenario—some seed-leaves look like good candidates.

6. Flying—why big craft should fly swiftly

In simple gliding, gravity provides the motive force, and energy to sustain the process comes from the steady loss of altitude; in soaring, the energy ultimately comes from atmospheric structures. In the sustained, active flight of airplanes, birds, pterosaurs, insects, and bats, the lift of paired wings again plays the key role. But sustaining altitude without that gravitational or atmospheric free ride demands some engine, typically either a propeller directing air rearward with a fixed wing deflecting the craft's airstream downward or else flapping wings that create both rearward and downward airstream momentum. Averaged over all but the briefest of time spans, the upward aerodynamic resultant must precisely equal the downward gravitational force, the weight of the craft, just as for steady gliding. So the same basic scaling rule appears applicable. As in eq. (10), weight divided by wing area, or wing loading, ought to vary directly with body length for an isomorphic set of fliers or, assuming constant density as well, with body mass to the 1/3 power. And similarly, bigger should mean faster; from eq. (11) we see that

$$v \propto (W/S)^{1/2} \propto l^{1/2} \propto m_b^{1/6}, \quad (13)$$

a specific prescription for how much faster larger aircraft must fly.

In a lovely book, Tennekes (1996) makes this a major point, drawing a single line on a graph that appears to indicate compliance (without even a shift in the constant of proportionality, 0.38 in SI units) from fruit flies to the largest passenger aircraft, a Boeing 747. Wing loading, W/S , goes up as the cube root of mass, m , and eq. (13) predicts cruising speed quite well. Other sources such as McMahon and Bonner (1983), Azuma (1992) and Dudley (2000) cite the same rule. Airplanes fit almost perfectly, at least if one excludes gliders and human-powered craft, which keep wing loading and therefore cruising speed deliberately

low. Birds fit the same regression line, wing loading again going up with mass^{1/3}, with both the same proportionality constant and scaling exponent.

Insects, though, scatter a lot more, with the scaling line recognizable only by lumping some very lightly wing-loaded butterflies and moths with heavily loaded beetles, bees, and flies and following downward the pre-established trend. Except for dragonflies, the insects we regard as smooth, fast fliers weigh several times more relative to their wing areas than the scaling relationship predicts—as do hummingbirds. Furthermore, eq. (13) predicts flying speeds considerably in excess (roughly double) what the all-too-feeble reliable measurements (and other considerations) show.

Why this fly-in-the-ointment? I think nothing especially obscure underlies the deviation. In a sense, the problem combines etymology and entomology (my apologies to the hummingbirds). The smaller the flapping flyer, the more the function of what we call a wing approaches that of a propeller and the less it resembles that of a paradigmatic airplane wing. In effect, a flapper uses its wings more often than does a fixed-wing craft. Indeed we see the greatest deviations from the rule where wingbeat frequencies are highest, more specifically, where the speed of the wings in their upstroke-downstroke oscillation most exceeds that of the insect's or hummingbird's forward flight. In effect, a flapper uses its wings more often than does a fixed-wing craft, and the speed most relevant becomes the tip speed of each beating wing rather than the forward speed of the craft. (alternatively, the area most relevant becomes the area swept by the wings in a stroke rather than the area of the wings themselves—"disk loading" thus replaces wing loading.)

So we need another parameter, the ratio of the forward movement of the craft to up-and-down wing movement. The propeller designers provide one, the so-called advance ratio, J , although for applicability to animal flight it has to be altered slightly—a wing swings, down plus up, through less than an angle of 360°, and its additional parameter, amplitude, can itself vary. As usually given for flying animals (Ellington 1984),

$$J = \frac{v_f}{2\phi nR}, \quad (14)$$

where v_f is flight speed, ϕ amplitude (or "stroke angle"), n wingbeat frequency, and R wing length.

Amplitude varies too little to matter here. Wing length, of course, goes down with size, which would push up the advance ratio. But small insects suffer more from the pernicious effects of viscosity and must make do with lower L/D ratios, as we saw earlier. So they have to beat their wings at high frequencies and fly slowly—their wings go up and down a lot for only a little forward progress—which more than offsets their small size. J for a bumblebee peaks at

about 0.66, for a black fly 0.50, for a fruit fly 0.33. By comparison, ducks and pigeons fly at about 1.0 (Vogel 1994). Halving the advance ratio roughly doubles the effective wing area, about what we see when comparing birds, which follow the scaling rule, with these fairly fast insects, which have greater wing loading and fly faster than it predicts. For the particulars of how small insects achieve frequencies that may reach 1000 s⁻¹—fabulously lightweight wings, special neuromuscular devices, and so forth—one should look at Dudley (2000) and other specialized accounts.

From the viewpoint of scaling, the relatively high flight speeds of some tiny insects—around 1 m s⁻¹ for a fruit fly (500 body lengths per second; a duck does less than 100)—might be surprising, whatever their obvious utility in an atmosphere that is rarely still. After all, their higher surface-to-volume ratios mean a relatively greater cost to deal with drag and a lesser cost to offset gravity. In fact, while true, the force needed to oppose drag remains modest—for a falcon less than 1% of weight or lift (Tucker 2000); for a teal (a duck) about 2% (Pennycuik *et al* 1996); for a desert locust, about 4% (Weis-Fogh 1956); for a bumblebee, 8% (Dudley and Ellington 1990); for a fruit fly about 10% (Vogel 1966). Those percentages, incidentally, suggest that drag reduction through streamlining can only marginally affect the cost and practicality of flight. Gravity remains the chief opponent.

7. The value of gravitational acceleration

Both whole organisms and their parts inevitably exceed the density of air—nature makes no blimps or ascending balloons. So any biological system that keeps a bit of atmosphere between itself and the earth's surface must contend with gravity. The particulars prove complex physically, complex biologically, complexly size-dependent, and at least occasionally counterintuitive.

One final example may persuade the reader of that last. We expect that a greater gravitational acceleration, as would characterize a larger planet, would make passively aerial organisms descend faster. That same increase in g , though, ought to increase atmospheric density—in one scenario (which we will assume) increasing directly with g (see, for instance, Taylor 2005). In the Stokes' law world of the small and slow, terminal descent speeds will indeed increase, because they depend on the difference between the densities of object and medium, and even doubling the latter will still leave it insignificant. The change in atmospheric density will not affect the all-important viscosity.

At Reynolds numbers above one, drag becomes increasingly dependent on atmospheric density (eq. 12) and decreasingly dependent on viscosity. Ignoring some complications, drag will vary directly with density. If both drag and weight vary directly with gravitational acceleration, then

drag-based terminal descent speeds will not – which strikes one as odd. By contrast, if lift also varies with density (eq. 11), then lift-to-drag ratios and glide angles (eq. 9) will be independent of air density. So the increased weight of a glider will make it descend faster – as in the drag-based Stokes' law range but not the drag-based higher Re range. Gravity always drives the aerial system earthward, but that does not imply inevitable importance for the particular value of g .

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