

Living in a physical world XII. Keeping up upward and down downward

STEVEN VOGEL

Department of Biology, Duke University, Durham, NC 27708-0338, USA

(Fax, 919-660-7293; Email, svogel@duke.edu)

1. Introduction

In defining an organism's immediate physical situation, one begins with position and orientation, just as when distinguishing between translational and rotational motion. Position always matters, even if no exact specification need be given for the pelagic or the aerial. Orientation can be ignored in only a few instances – non-motile spherical unicells in a continuous medium, perhaps a colonial *Volvox* in a pond, under some circumstances maybe bird eggs and round nuts.

We ordinarily treat orientation mechanisms as matters of coordination, putting them in treatments of neurobiology. Detectors, such as proprioceptors, provide information with which nervous systems direct appropriate muscular activity. We less often look at the underlying physical situations, at potential perturbing forces, at the options available for reorientation, and at devices for maintaining orientation. (But I must immediately applaud a symposium held a few years ago, reported as Fish and Full 2002.) One essay certainly cannot do the subject justice – especially since we know quite a lot about the subject in a somewhat scattershot way – but perhaps the main bases can be touched.

Elementary textbooks of physics recognize three mutually exclusive situations, ones in which bodies in their positions subject to a gravitational (or analogous) force are either stable, unstable, or neutral. As in figure 1, the distinctions hinge on differences in either their own mass distributions relative to their footprints or on the contours of the supporting surfaces. (The issue of substratum contour will be put aside as a second-order one, left for the time being to people concerned with behavior.)

A neutrally stable object simply has no preferred orientation. At most, perturbation adds rotational momen-

tum, which then keeps the thing rotating. The commonest neutrally stable objects are rigid cylinders (one neutral axis) and spheres (two such axes) lying on rigid surfaces, and objects in continuous media whose centers of gravity coincide with that of the fluid they displace. I will say no more about these latter cases, relatively uncommon among macroscopic systems, simply noting that neutral stability opens a possibility for ground-level wind dispersal – one exploited by, at least, Russian thistles (tumbleweeds) in the drier parts of North America.

Almost all our passive possessions are stable around at least two axes – tip one a bit north or south, east or west, and it returns by itself to its previous orientation. Most often this comes about because the work of perturbation raises the object's center of gravity, and the gravitational restoring force then drives its subsequent reorientation. Put another way, the perturbation generates a restoring force, and the system enjoys the resulting negative feedback. For instance, we make pencils with hexagonal cross sections to stabilize their rotational axes. Petroski (1990) describes the origin of the practice, one especially handy for cultures with sloping desks. By contrast, while an unstable object may be stationary, any perturbation will upset the balance and produce runaway reorientation – a process with positive rather than negative feedback. As we will see, seemingly impractical, even dangerous, precariousness turns out to be widespread among living organisms.

“Stable” and “unstable” positions require quantitative qualifiers if one considers all but minimal perturbations. Turn a stable object far enough and it ordinarily becomes unstable, so if need be one could plot, say, turning moment against angle, with the shift from stable to unstable marked by the angle at which the moment dropped through zero. This kind of static stability requires another note as well,

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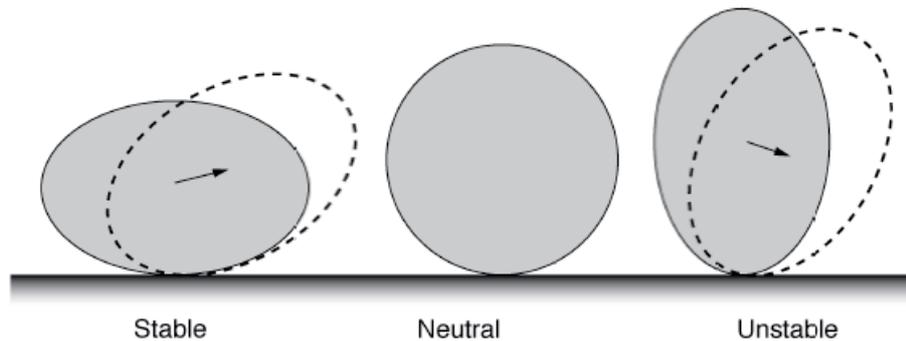


Figure 1. The stability of three gravitationally-loaded rigid bodies on horizontal, rigid substrata – assuming, of course, uniform density and no other forces.

something to bear in mind. Most often the downward force of gravity enforces resistance to lateral perturbing forces, but any other unidirectional and externally applied force would do. Whatever the origin of the force, crucial to the shift of orientation are lines of action and their moment arms.

For many biological situations, this static view proves inadequate. Often we need to consider dynamic stability as well. Acceleration in effect tips the direction of the restoring force, and it may shift its line of action as well. The speed of application of a perturbation commonly bears on its consequences and the effectiveness of any active response. As does the duration of a period of instability; for instance, that of any airborne phase of a terrestrial gait. The activities of an organism itself can either produce or offset instability – one thinks immediately of the location of control surfaces on swimmers and fliers relative to their centers of mass, buoyancy, and pressure. Responses to perturbation can be sluggishly overdamped or sufficiently underdamped to permit transient, sustained, or even increasing oscillations. Problems of dynamic stability have bedeviled vehicular design at least since wheelbarrows came into use, in China, over a thousand years ago.

2. Static stability – sessile systems

For sessile organisms well attached to substrata, the issue of stability in the present sense remains moot. Only attachment strength, along with the magnitude and line of action of any lifting force and vulnerability to peel failure, hold consequences for a limpet, snail, mussel, or waterpenny beetle on a rock. In moving water, only a few sessile organisms, such as flounder (plaice), manage to hold position without some secure attachment, and these are neither erect nor exposed to especially rapid flows. Among sessile terrestrial ones, including some of the largest, though, remaining in place may rest on gravitational stability.

Many, probably most, terrestrial plants manage to attach themselves to the ground with sufficient strength to resist

the turning moment of wind-induced drag. But reliance on well-ramified, tension-resisting roots becomes ever more problematic with increasing size. Greater height increases both the speed of local winds and the turning moments they cause. And a greater area of foliage raises the drag caused by a given wind. However one assumes that attachment effectiveness scales, it will most likely increase with a lower exponent than that moment. Some quite large plants do appear to manage mainly by ground-grabbing, most notably bamboos and tropical trees that can take advantage of an ample general tangle of roots in the soil. Some, where I live most notably large specimens of the loblolly pine (*Pinus taeda*), limit turning with a stiff, deep, central taproot, essentially a downward extension of the trunk.

Essay 7 (Vogel 2006a) considered a tree that resists uprooting, not by attachment to the ground, but by being gravitationally stable. With ample weight, a low or deflection-resistant center of gravity, and a wide, stiff, partially buried base, the “up-” in “uprooting” takes on an especially literal significance. When such a tree does uproot, the lower portion of the trunk commonly rests a meter or two above the ground. Figure 2a shows such a tree, one that grew in a fairly open and unsheltered location. An instructive variation of the arrangement has repeatedly appeared in trees that live in the shallow water of swamps. Weight near the base, where it will not move laterally when wind-loaded, increases stability most effectively. But what matters is effective weight, that is, weight less buoyant force. The densities of almost all fresh woods lie below that of water, and even the few denser ones are not much denser. So trunk volume below the water line has little stabilizing value – and these trees produce conspicuous trunk enlargements just above the water, as in figure 2b.

3. How to stand on legs

A tripod can be stable if its center of gravity falls in the area defined by three straight lines with the legs at their ends.

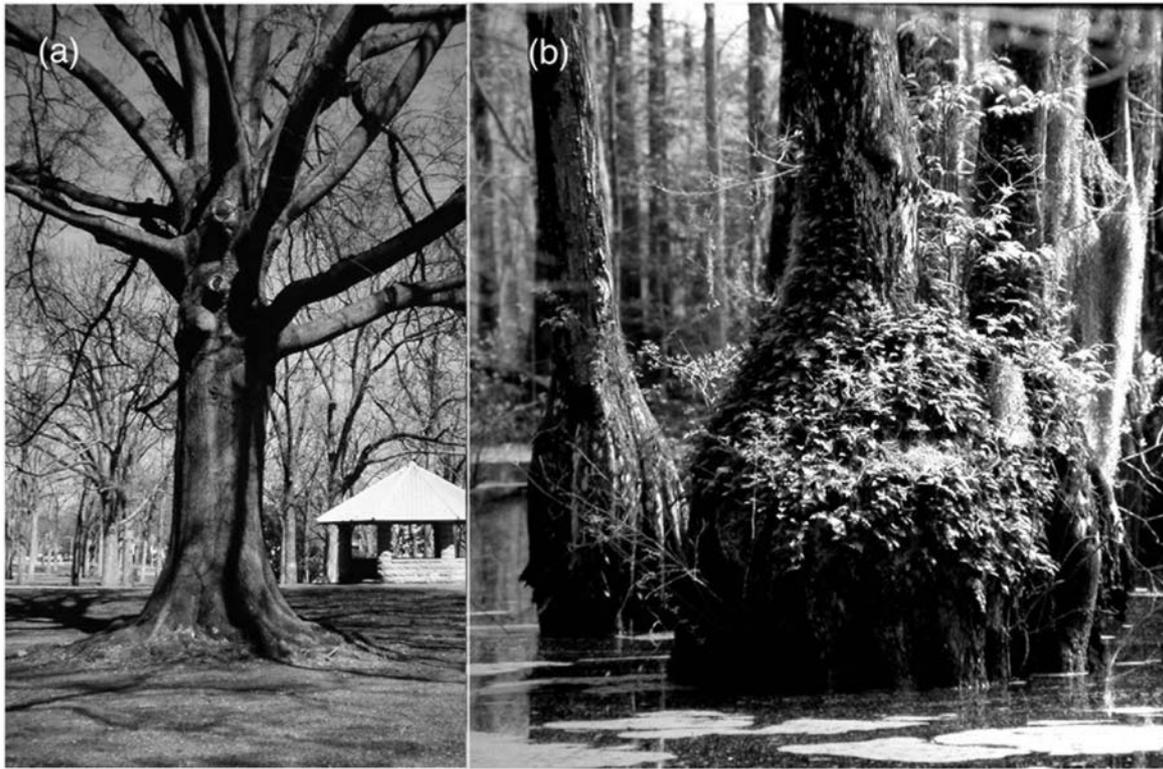


Figure 2. (a) The lower part of a willow oak (*Quercus phellos*) grown in a fairly exposed location. (b) The lower part of a baldcypress (*Taxodium distichum*) in the shallow water of a coastal swamp in North Carolina, USA.

Additional supporting legs merely increase the number of lines needed to establish that area, assuming flexibility of leg length or joints or else substrate compliance allows the extra legs to make useful ground contact. Naively, then, we might assume that unipeds (as are some standing birds) and bipeds (ourselves) are unstable when standing, while quadrupeds, pentapeds (kangaroos, at times), and yet more leggy creatures can stand stably. That assumes amply stiff joints, a boundary condition effectively defining the other end of biological reality. In fact unipeds and bipeds need not be intrinsically unstable since feet can provide sufficient contact area to circumscribe the line of action of gravitational force. But for them stability does demand broad, stiffly articulated feet. The instructive exception, not hard to experience, consists of standing on stilts – virtually impossible without fairly frequent changes in contact points.

Since no animal in nature engages in bipedal stilt-standing, no standing animal need be intrinsically unstable. Yet however easily achieved, few if any standing animals take full advantage of stable postures. Even we humans, while we appear to stand directly over our feet with our weight borne by compression of our leg bones, deliberately court instability. We tilt slightly forward and then offset that shift of center of gravity by muscular action, principally

through tension in the large muscles of our calves and the backs of our thighs. (Hasan 2005 describes the remarkably complex system involved.) We – and most (perhaps all) erect quadrupeds – continuously sense position and adjust the output of our tonic muscles. Sensing is critical, carried out, as Sir Charles Sherrington (1906) pointed out a century ago, by an elaborate proprioceptive system that signals forces and lengths of muscles. We pay scant attention to its operation unless doing something mildly unnatural such as standing for a prolonged period on one leg. Toy horses, cows, and humans stand only precariously; real ones are not such easy pushovers.

Standing posture varies systematically with body size in a way that makes sense for a slightly unstable system which does not profligately produce force and work for continuous corrective movements. A large mammal stands almost perfectly erect, clearly bearing nearly all its weight on the lengthwise bones of its legs. A small mammal stands in a crouch, with leg joints flexed to one degree or another. A crude rationale goes as follows. Muscle makes up about the same fraction of body mass of all mammals, and the contractile force a muscle produces varies with its cross-sectional area. So, all else equal, the small mammal can exert more forceful corrections and maintain a less bone-

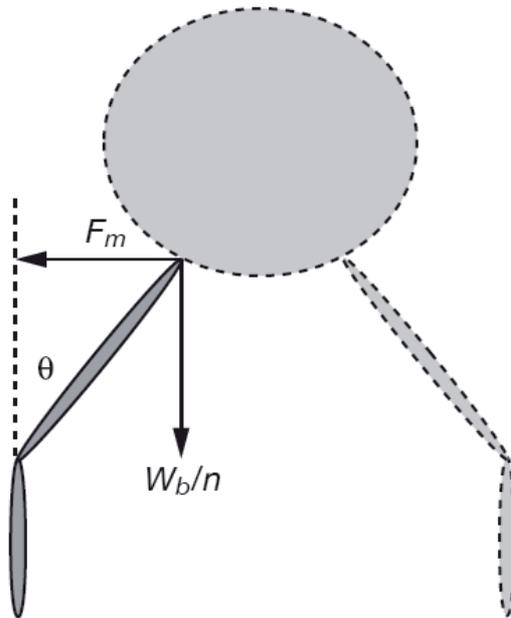


Figure 3. Adjoining long bones of a standing animal with the flexion angle, θ , between them. W_b is body weight; F_m is the force the relevant muscles must exert to offset the flexion; n is the number of (identically loaded) legs.

supported and more unstable posture relative to its body mass. If, as in figure 3, a joint is flexed by an angle, θ , body weight is W_b , and muscle force is F_m ,

$$\frac{F_m}{W_b} \propto \tan \theta. \quad (1)$$

F_m scales with the square of body length, W_b scales with length cubed, so their ratio must scale inversely with length and, assuming creatures of similar shape and density, force relative to body weight should vary inversely with length or $W^{-0.33}$. Thus (with constant gravitational acceleration), flexure angle should vary as

$$\tan \theta \propto M_b^{-0.33}. \quad (2)$$

While I have not seen a direct test of the prediction, Biewener (2003) predicts and supports a similar one, taking a somewhat different approach. He cites data that give $M^{0.26}$ for “effective limb mechanical advantage,” close to the inverse of the flexure angle used here – the difference between 0.26 and 0.33 is unlikely to be significant. He notes (and I completely agree) that, by lowering the center of gravity, a flexed stance confers advantages when an animal accelerates, both for linear and angular acceleration. In short (one might say), it imposes a cost in stability – more forceful corrective motions – but enhances maneuverability.

One predicts, therefore, that the height when standing of a mammal’s center of gravity with respect to body mass will vary with an exponent less than the 0.33 of

isometry – a rationale for our common observation that small mammals are on average long and stand low, big ones are short and stand high. Anticipating just a bit, the flexed stance and concomitant change in muscle location also lower muscular efficiency in locomotion. Muscle does best if shortened slowly, as measured in muscle lengths per unit time – “intrinsic rate of contraction”. But the advantage in this respect of smaller size normally gets offset by the higher stride frequency of smaller animals. Add the size-dependent variation in location, and the small animal needs higher intrinsic rates and has to pay a higher price in cost of transport, energy relative to mass moved times distance.

Cows, as expected, stand on almost unflexed legs. A practice termed “cow-tipping” enjoys a widespread body of folklore, at least in the United States. Supposedly one or a few people who sneak up at night on a sleeping, standing cow in a field can push it over, with distinctly detrimental effects on the animal – taking advantage of the narrow window of stability consequential to a high center of gravity and closely spaced legs. An analysis by Lillie and Boechler, at the University of British Columbia, (2005) concludes that a standing cow has sufficient stability to require an impractically large force for such a prank, about 3000 N (equivalent to 300 kg). Thus if single human can push about 300 N at the requisite height, ten synchronized pushers would be needed. (Lillie and Boechler assume what I think is an overly generous estimate of the push a typical human can exert; Cotterell and Kamminga 1990 cite a datum for maximum pull of 280 N, which ought to be about right for pushing as well and which I have just rounded off).

Pushing force, though, may not be the key constraint that renders the stories apocryphal. More importantly, cows do not sleep standing up, and when standing, they have the usual dynamic instability and ever-vigilant reflexes that one experiences if one tries to tip over a dog or cat. If the cow can respond by modestly widening its stance, even without an overall shift of its center of gravity, about 4000 N or 14 pushers would be needed – quite a challenge to deploy without excessively disturbing the cow. As Young-Hui Chang has found (personal communication), even a flamingo that stands quietly on one leg above a splayed foot makes continuous minor muscular adjustments as directed by its proprioceptive system.

4. And how to walk on legs

Moving about on legs adds other destabilizing factors. Indeed, for most forms of legged locomotion requiring continuous stability would greatly limit motions and gaits; and in practice most such systems are at least slightly unstable most of the time. Two unavoidable factors loom largest. First, progress demands pushing rearward on the

substratum, ensuring that the line of action of the propulsive force lies below that of the resistive forces of inertia (resisting acceleration) and drag (resisting speed). Second, moving demands that at least one leg be lifted from the substratum, so an animal must be supported by one less than its normal complement.

That mismatch between an animal's rearward push and the resistance to that push produces a moment that turns the animal head-backwards. In practice, a forward shift of the center of gravity provides the compensatory head-forward moment. Acceleration, most notably at the start of a walk or run, takes more of a shift than does moving steadily; with only minor air resistance for most forms of terrestrial locomotion getting mass into motion greatly exceeds drag as an impediment. One leans forward when walking with the greatest tilt when one starts, and walking when half submerged in water (more resistance, less gravitational force) takes a greater tilt. We start walking by deliberately falling forward, and we cannot stand in quite the same posture we use while walking at anything over the most modest pace. Adding resistance by asking that a person push or pull makes matters worse, eliciting the same response, an increased forward tilt.

Increasing the number of legs from two to four does not solve the problem, although it may make it easier to manage by not demanding that the center of gravity shift to a statically unstable location. So asking that a quadruped push or (more commonly) pull still exacerbates instability. At one time horses were often harnessed to the carriages of the ostentatious with checkreins that kept their heads high. That limited their pulling abilities and obviously distressed them. A 19th century children's classic, *Black Beauty* (Sewell 1877) made much of that and other abusive practices and probably contributed to its abandonment.

When walking, bipeds such as ourselves sway slightly from side to side as one shifts support back and forth from one leg to the other, again displacing support from beneath the center of gravity. Again, one cannot stand in most positions one assumes while walking at all but the slowest speed – snapshots of standing postures cannot be arranged into a walking sequence. Thus to fore-and-aft we add lateral instability, although the latter averages out over time. At least lateral shifts put the line of action of the center of gravity closer to the ground-contact point of the leg that will then take the load and provide propulsion. Penguins, relative to their heights the shortest-legged of birds, sway the most; they use the gravitational shift as part of a pendulum-like energy minimization scheme (Griffin and Kram 2000). That sway characterizes a quadrupedal gait called “pacing” or “racking” in which both right and then both left legs move simultaneously. Horses can be taught to pace; long-legged giraffes and camels normally pace, most likely because these long-legged animals can then use greater leg-swinging

angles without front-hind interference. Pacing, of course, imposes the same instability as bipedal walking, losing a major advantage of quadrupedalism. Still, both some especially short-legged walkers and some especially long-legged walkers sway – if for different reasons.

A variable called “duty factor,” the fraction of the time a given leg provides support, helps us judge whether stable locomotion is even possible. A two-legged walker cannot be fully stable even at a duty factor of 1.0 – standing still – as already noted. Oddly enough, that does not demand that bipedal walkers have a continuously vigilant and actively intervening proprioceptive system. Small wind-up walking toys or similar unpowered downhill walkers do quite well, although they usually have feet of biologically unreasonable areas. Their centers of gravity may never lie directly above a leg, but properly timed foot-falls limit falling to one side or the other. Coleman and Ruina (1998) have devised a more elaborate version of such a self-compensating downhill walker, a physical model that can be put together from widely available toys (“Tinkertoys”), as well as a theoretical treatment of this kind of stability-while-in-motion. Powered versions (Collins *et al* 2005) walk with efficiencies comparable to those of walking humans with only the most minimal control.

A four-legged creature can be stable, but only if it never has more than one leg off the ground, that is, if the duty factor equals or exceeds 0.75. And it can do that only if it shifts its center of gravity slightly by, say, tilting the body, away from whichever leg is held aloft, as in figure 4, keeping the center of gravity over the triangle formed by the contact points of the remaining legs. In effect, a leg has to give the ground a slight body-tilting push just before breaking contact. Quadrupeds do walk stably (postural reflexes aside), but mainly when they go quite slowly, as when stalking prey. We might expect slow walking to demand rather than merely allow static stability, but work on chelonians – turtles and tortoises – tells us quite the opposite. While duty factors generally run well over 0.75, Jayes and Alexander (1980) found that at times only two feet contacted the ground. They provide a persuasive (if counterintuitive) argument that eschewing stability permits slower and more efficient muscle action.

But slower locomotion does impose a lower tolerance for instability. As Alexander (2003) notes, while forces need only balance when averaged over a stride, during any unstable period an animal falls with gravitational acceleration, g . And some relatively constant fraction of leg length, h , must limit the permissible falling distance. As an indicator of the need to preserve stability, he suggests a dimensionless expression based on these variables and on stride frequency, f :

$$\frac{g}{2f^2h} \quad (3)$$

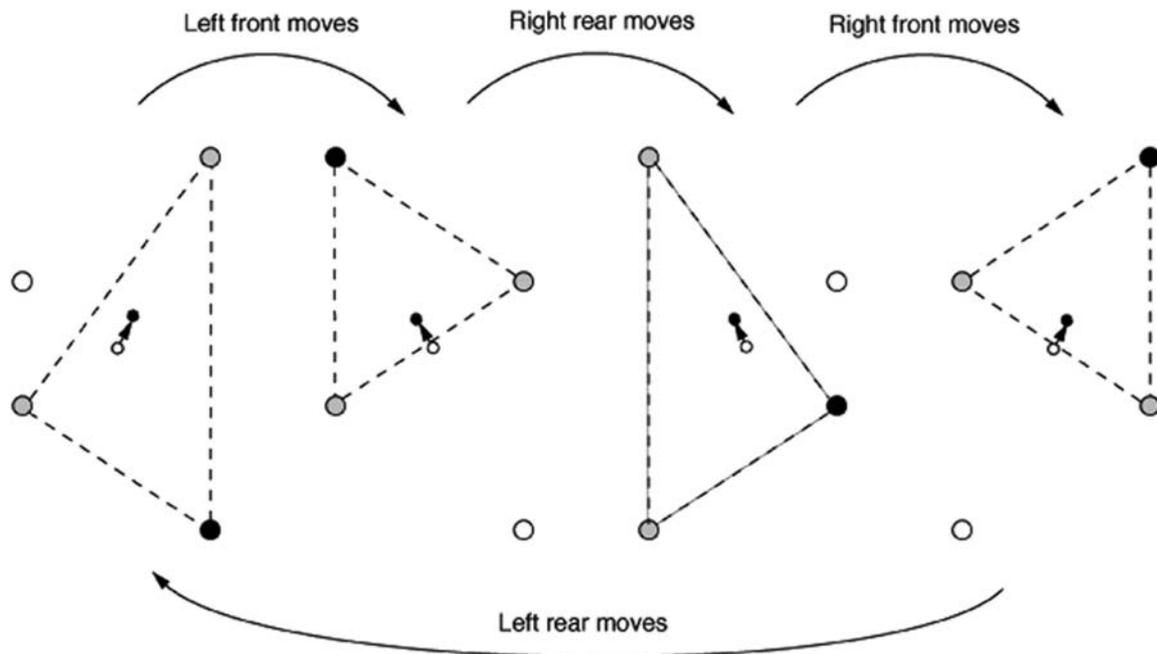


Figure 4. The normal stepping pattern for a quadrupedal walker. The most recent footfall is shown dark, the one just lifted is light. Arrows indicate shifts of the center of gravity needed to move it from the center of a standing stance to equivalent positions with respect to a line between diagonally opposite supporting legs.

Thus instability becomes more tolerable as an animal increases its stride frequency, especially if this can be done without much of a concomitant decrease in leg length. Put in practical terms, at low speeds and thus low stride frequencies, stable gaits work better; as speeds increase, unstable gaits become ever more practical and higher degrees of instability more tolerable. Dogs can tolerate a lot of instability when galloping but less when walking; turtles, low to the ground and making infrequent strides, should be much less tolerant of instability – although, as just described, they can still be unstable.

Alexander's (2003) approach parallels a suggestion I made (Vogel 2003) about the minimum speed for galloping, also based on maximum fraction of leg length that an animal can fall between foot-falls. I invoked the Froude number as a predictive variable; expression (3) amounts to the reciprocal of the Froude number (Fr) if animals swing their legs similarly, so speed is proportional to the product of stride frequency and leg length, fh :

$$Fr = \frac{v^2}{gh}. \quad (4)$$

Six legs permit unconditional static stability. A hexapedal animal need only support itself on alternative triangles, and a duty factor of 0.5 is ample. Insects, paradigmatically hexapedal, use such a stable gait at low speeds but become increasingly unstable as they move faster (Ting *et al* 1994). (Of course not all insects walk on all six legs – for instance,

praying mantises and mosquitoes use only four of their six.) At the highest speeds some, such as cockroaches and ants, have fully aerial phases (Full *et al* 2002) – as we do when running. Further increase in number of legs further reduces the maximum duty cycle consistent with stability, but six legs are the fewest paired legs that enjoy the option of fully stable walking without shifting centers of gravity. That has stimulated considerable interest in the way insects walk and run by designers of walking robots and robotic vehicles.

5. The stability of aircraft, living and non-living

An object standing or moving on the earth's solid surface faces two planes of potential instability, both vertical, resulting from the way its center of gravity lies above the point of contact with the substratum. For bilaterally symmetrical movers these planes are side-to-side and fore-and-aft. Alternatively, we can adopt anatomical practice and designate them transverse (or frontal to the human anatomist) and sagittal.

Devices moving through continuous media encounter in addition a horizontal plane of potential instability, frontal to the anatomist (except ones dealing with upright humans). For names we normally turn to the world of airplane design and performance, perhaps to avoid ambiguity about whether changes within any of the planes refer to changes in position (translation) or, as here, changes in orientation (rotation).

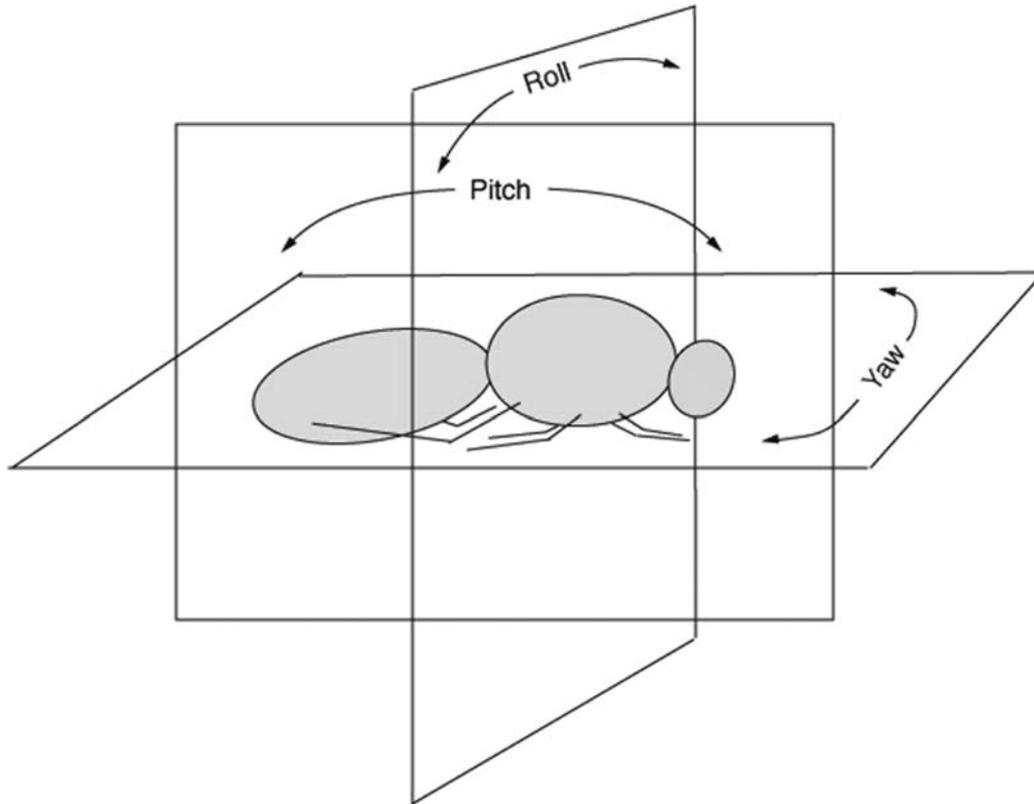


Figure 5. The three planes in which a flier can turn.

As in figure 5, that community defines the planes “roll” for the transverse or sideways-tipping, “pitch” for fore-and-aft rotation, and “yaw” for this last side-to-side swinging in a horizontal plane.

Dealing with three planes complicates both achieving directional control and analyzing how organisms might be managing just as it amplifies the importance of the matter. (In fact, perturbation about one axis commonly affects orientation about a different axis, introducing another, and a quite common, element of instability.) Putting aside degree of stability, a stable aircraft returns to its previous orientation after a perturbation without active adjustment of its controls. An unstable one either does not return or deviates even further – in whatever plane is at issue.

In a short article in *Evolution*, in 1952, John Maynard Smith drew attention to the considerable orientational instability of most extant flying animals. Maynard Smith, before taking a degree with the great evolutionary biologist J B S Haldane, had spent some time as an aeronautical engineer, so he brought a new perspective on flight to both paleontologists and physiologists. He compared present-day insects and birds and the mature pterosaurs to the earliest then-known flying ancestors of each. (He had inadequate information about early bats.) He suggested that, as active flight developed in each lineage, evolution produced ever

less stable designs. In particular, control in pitch appeared, as with aircraft, to present the greatest challenge. Early forms tended to have greater development of horizontal surfaces on their rear portions – lateral plates on insects such as the dragonfly-like Paleodictyoptera, lateral membranes on the pterosaurs, and large tails on the birds – that stabilized flight much as rear feathers stabilize our arrows. He noted that while many extant birds have large tails, most deploy them mainly for take-offs and landings, when tails lower the stalling speed and thus facilitate operation without runways. (The remarkable pictures in Dalton 2001 provide graphic illustrations of just this.)

What permitted the instability was the concurrent evolution of ever more competent flight control, that is, of neuro-muscular systems. What drove the process was the inherent trade-off in flying machines between stability and maneuverability – a much less forgiving but essentially identical situation to that faced by legged locomotion on land. That contemporary birds are quite unstable renders them dangerously flawed models for human aircraft. Many early attempts to build airplanes foundered from inadequate appreciation of the fact. At least one case proved fatal, that of Otto Lilienthal, in 1896, author of the pioneering analysis, *Bird Flight as the Basis of Aviation* (1889), and pilot of what we would call hang-gliders. Others, notably Samuel

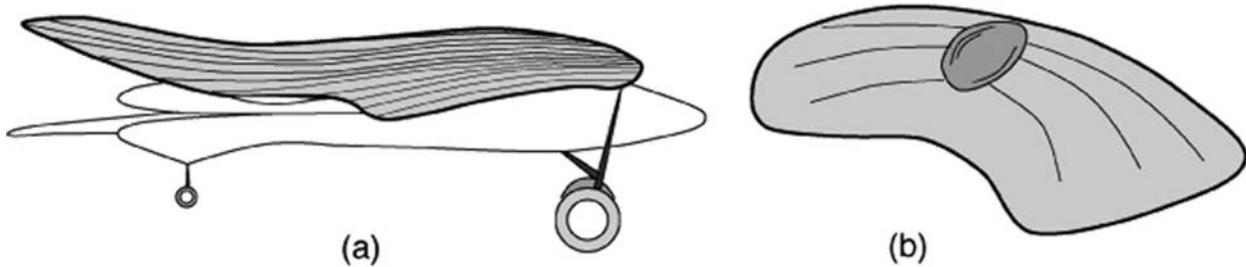


Figure 6. (a) The Etrichs' glider of 1906, traced from a photograph of a full-scale model at the Owl's Head Transportation Museum, Rockland, ME; struts and cables have been omitted. (b) The seed-leaf of *Alsomitra*.

Langley, took great pains to assure pitching stability – the most troublesome plane and the one that doomed Lilienthal. Langley's best full-scale airplane, which failed (at least) from structural weakness, achieved inherent pitch stability with tandem wings, one pair behind the other.

Unlike Lilienthal and others, the Wrights gave considerable attention both to stability and to control by adjustments of the aircraft rather than the position of the aviator (Culick and Jex 1987). Their later gliders and 1903 Flyer had sufficient stability to be safe and reliable in breezes but not so much as to compromise control. Indeed, the only fundamental change made thereafter consisted of substituting for the canard wing in front the now familiar pitch-controlling horizontal tail. Canard wings persist only in a few high-performance aircraft (usually with fast-acting computer control offsetting intrinsic instability) and possibly as the “hammerheads” on sharks in the genus *Sphyrna*. On the latter, they may (a good study is overdue) facilitate following the contour of the sea bottom or suddenly lunging downward. The “bow-rudder,” a front paddle directed obliquely forward by white-water canoists approaching rocks, works the same way except in yaw.

Stable fliers do exist in nature, as one might anticipate, where active control remains out of the question. As with terrestrial stability, plants provide the exemplars. A descending, autogyrating samara of a maple or other tree must be able to recover from the perturbations of wind gusts or branches encountered on route. Non-autogyrating gliders, closer to airplanes or gliding birds, are rare. The most famous is the gliding seed-leaf of the Javanese cucumber *Alsomitra* (formerly *Zanonia*). As with so many phylogenetically odd animal gliders it lives only in the understory of the especially high dipterocarp forests of southeast Asia – perhaps because the nearly still air found there spans an unusually great height range. It provided a model for some early aircraft, those of the Etrichs, who built a series of *Zanonia*-winged craft, beginning with gliders (figure 6), in the first decade of the 20th century. Most likely as a reaction to Lilienthal's death, they wanted assurance of stability. Which they achieved, producing a glider that was almost unmaneuverable (Bishop

1961). Vincenti (1990) provides a fine historical perspective on the gradual appreciation of the issues involved.

They thereby inadvertently sacrificed straight-line performance. Putting that tradeoff in context involves the so-called lift-to-drag ratio of an airfoil, hydrofoil, or propeller blade. In effect, such a device generates lift (L), a force normal to its motion through the medium, at the price of an increase in drag (D), the force tending to retard its motion. The ratio not only represents a kind of efficiency, but it translates directly into the range a glider can go in still air. It does this by setting the “glide angle,” θ , the angle with respect to the horizontal, at which a passive craft will descend:

$$\cot \theta = \frac{L}{D} \text{ or } \tan \theta = \frac{D}{L}. \quad (5)$$

Gliding thus maximizes distance by maximizing L/D , which varies somewhat with speed. It produces the greatest time aloft at a slightly lower speed and thus a slightly lower (but maximal for that speed) L/D .

The *Alsomitra* seed-leaf in nature develops a relatively poor lift-to-drag ratio, 3.7, almost certainly in the interest of stability. In a wind tunnel, its optimum (at the price of some stability) is still a mediocre 4.6, about half of what an insect wing under equivalent circumstances can reach. Its swept-back wings put the seed and center of mass lie ahead of the aerodynamic center (the point of action of the lift-drag vector), so it has the equivalent of the expected tail. As a result, the increased lift of any inadvertent upward pitch of the nose is far enough aft to offset rather than amplify the perturbation. And normal operation at an angle of attack well below the stall point gives extra margin for that stabilizing effect. (Azuma and Okuno 1987; Azuma 2006).

Birds, by contrast, fly as remarkably unstable craft – one cannot easily launch a stuffed bird on a smooth and fairly flat path. As a result, it has been argued (Harris 1989) that their use as models hampered the development of airplanes. Still, the degree of instability varies a lot; and, again, varies more-or-less with maneuverability. The *Alsomitra* seed-leaf accepted a lower-than-ideal lift-to-drag ratio in the interests

of stability; birds make analogous departures from best performance in the interest of maneuverability. Other things equal, a longer, narrower wing gives a higher ratio than does a shorter, broader wing – again something glimpsed but not always appreciated by earlier aircraft designers. Why, then, do sea birds have particularly long and narrow wings while those that glide over land are shorter and wider, with splayed primary feathers instead of pointed tips? These terrestrial gliders apparently accept a lower best L/D – in effect a lower efficiency – and thus steeper minimum glide angles in order to be able to turn more sharply and thus fly in tighter circles. That should be important when gliding in an ascending thermal torus or an updraft over irregular terrain. Stabilizing against yawing – more important in the more erratic winds over land – has been suggested as another function of splayed primaries (Pennycuik 1975), but with little hard evidence of either that action or its utility.

Terrestrial birds also gain in ability to fly slowly without stalling – increasing the angle at which wing meets air to boost lift (which varies with the square of speed) at low speeds – and thus the ability to land and take off at near zero airspeed. (Norberg 1990 give a good review of the contrast.) Enhancing that low speed performance, terrestrial soarers have lower wing loading (W), the ratio of weight (mg), to wing area (S):

$$W = \frac{mg}{S} \approx \frac{L}{S} \propto \frac{v^2}{S}. \quad (6)$$

Weight to be supported translates into lift – roughly, since lift is conventionally defined as normal to flight direction rather than to the horizon. The lift required to offset body weight depends, again roughly, on the square of flying speed. So lower wing loading implies a lower weight-sustaining minimum flight speed.

Note that L/S in eqn 6 scales with linear dimensions – lift here is lift required to support weight, not lift as proportional to wing surface at constant speed. That scaling makes wing loading higher for a larger but otherwise similar flier. Such scaling underlies not only the non-similarity of fliers of different sizes but also the higher flying speeds of larger craft – with their associated diminution of maneuverability as well as their higher takeoff and landing airspeeds and higher weight-specific power requirements for sustained flapping flight. Thus the 70 kg extinct bird *Argentavis magnificens* had to soar and could live only in a region of steep slopes and high winds (Chatterjee *et al* 2007).

While equipped with nothing analogous to the splayed primaries of terrestrial soaring birds, the same trade-off has been recognized in bats by Aldridge (1986), Norberg and Rayner (1987), and Dietz *et al* 2006). Bats that fly through forests have shorter, broader wings, and they weigh less relative to wing area so they can fly more slowly – paying a price in power (in effect overall performance) for that

maneuverability. By contrast, bats that fly in open areas have longer, narrower wings, more weight relative to wing area, and they fly faster and more economically.

Like birds and bats, flying insects are fairly unstable. Extant forms lack aerodynamic stabilizers such as tails or abdominal protrusions; in any case these latter would be of limited service during hovering. Hind legs sticking out into the airstreams of the two wings seem to give some ruddering action in some forms, and mobile abdomens (as in many wasps) provide at least the possibility of adjusting centers of mass and drag. As Dudley (2000) notes, the way the wing stroke centers above the body, with wings almost (or actually) touching at the top but not the bottom of the stroke, provides some degree of stability in both roll and yaw. (The torque induced by a center of lift and thrust above the center of drag should matter little for a flier that can control the direction of the resultant of lift and thrust.) And the elongation of bodies fore and aft – heads and abdomens, the latter sometimes quite long – should give a bit of pitch stabilization, at least for transient perturbations.

The issue of stability may bear on the origin of flight as well as on the subsequent evolution of flying lineages. As pointed out by Ellington (1991) (and summarized by Dudley 2000), a long, circular cylinder, held obliquely, can descend at glide angles as low as 40°, no worse than some non-flying but gliding vertebrates. Instability, though, wrecks the scheme at all but Reynolds numbers (length times speed, in effect) still lower than those of flying insects. The difficulty traces to an aerodynamic center in front of the center of gravity, meaning that any upward pitch will be magnified until, at equilibrium, the cylinder will descend vertically while oriented horizontally, parachuting rather than gliding. Small winglets protruding from the sides – minor cuticular extensions for insects – and located toward the rear fix the problem, making the cylinder stable in pitch. (Moving the center of gravity forward, where it is in extant insects can help also.) Yawing stability can be achieved by adding a caudal filament, and roll stability as well comes if a bilateral pair of diagonally rearward-pointing cerci replace the filament. Of course overdoing the appliances on the rear end produces the equivalent of a fletched arrow, which will both descend and be oriented vertically and thus have the maximal drop speed and gain no horizontal distance at all.

In effect, a flier picks some combination of three variables, stability, maneuverability, and performance, each in practice multidimensional. As we have seen, both the exceptional stability of the *Zanonia* seed-leaf and the maneuverability of terrestrial soarers come at a price in level-flight performance. In general, an increase in any one of the three variables extracts a price with respect to one or both of the others. None, though, lend themselves to definitions that combine precision with practicality, and designers face no definitional limit to what a particular combination can

do. Birds and bats, as D E Alexander (2002) points out, may be less constrained in that choice than insects and human aircraft since they can vary wing geometry quickly and extensively.

6. The inputs for aircraft

Only with adequate control systems can instability be tolerated, much less capitalized upon. Proprioceptive feedback loops, gravity and acceleration detectors, and associated anticipatory and dynamic devices permit walking, running, climbing, and all manner of terrestrial acrobatics. However complex these tasks, they pale before those of control in continuous media. And the less stable the flier or swimmer, the greater its dependence on control. Moreover, even a stable flier faces at least two problems practically unknown in land-based locomotion. First, air and water cannot be relied upon to remain at rest with respect to the earth, that is, to their underlying solid substrata. Thus sensing what goes on in an animal's immediate vicinity may limit clues to its overall motion. The slower the animal, the lower its speed through the local medium relative to motion of the medium itself. So the problem must bedevil organisms more than it does our boats and aircraft. And second, heading provides only a limited cue about course. Face north and move forward at 1 m s^{-1} in a wind or current from the east at the same modest speed, and you actually progress northwest at 1.4 m s^{-1} .

Small airplanes (excluding high-performance military craft) are, by design, about as stable as they can be without overly compromising their ability to make necessary changes of direction. The new pilot learns, in the words of Molly Bernheim (1959) that when things go awry, "Let go! The airplane can look after itself better, now, than you can do! Turn it loose! Then, and only then, you may guide it gently where you want it to go." Even so, airspeed and ground speed may be quite different, and heading may not equal course. Moreover, our land-based sensory equipment can mislead us. For instance, semicircular canals cannot reliably separate gravitational from angular accelerations. So a banked turn feels no different from straight flight, and the pilot must read the instruments, not the receptors medial to the seat of the pants.

How then do animals get the sensory input critical for active control? Visual signals provide widely used references for both orientation and location, and both birds and insects typically have large brain areas devoted to processing visual input. The horizontal cells of bird retinas have been known at least since the work of the great neuroanatomist, Ramón y Cajal, a century ago; they purportedly select horizontal lines for attention in a process of horizon-detection that would distinguish level flight from banked turns. Were night-flying birds, insects, and, of course, bats not so common and

accomplished, one might declare visual input essential – which it certainly cannot be. Equipping an enclosed volume of air to work as an altimeter should be simple enough; a human acquires a pair that can be painfully effective on airplane flight with plugged Eustachian tubes. (And swim bladders can signal depth changes in fishes.)

The flight motors of insects, on which work has been extensive, have at least three additional sources of sensory input. Bending of antennae and setae equipped with mechanoreceptors at their bases provide information about local airflow, including, most likely, the airflow on each side caused by the wings themselves. Additional mechanoreceptors on the wings and in cuticular structures adjacent to them can not only signal what the wings are doing but, because of the non-rigidity of all the relevant structures, can provide feedback on the loads the wings encounter. Since oscillating wings act as gyrosensitive devices, the receptors should receive dynamic inputs. Several groups of insects, most notably the true flies (Diptera) have developed gyrosensitivity further, converting one pair of wings (the hindwings in Diptera) into stalks with knobs on their ends that still oscillate as if wings. Finally, the flexible connections between thoraces, housing the flight motors, and both heads and abdomens, permit the latter to provide inertial information – as, for instance, when a turn is initiated either volitionally or inadvertently. Dudley (2000) reviews what has been done in an active area that at this point seems to lack a good synthesis.

The principal difficulty for both flying animals and our understanding of how they manage, is the lack of an obvious source of earth-referenced data. Vision cannot form the sole such source, but sensing cuticular deformation can do little to augment it, particularly in a domain in which ambient winds rival or even exceed flight speeds and in which the variations that we lump as local turbulence cannot be easily averaged over time or space. People investigating bird migration – which I want to skip over here – have wrestled with the problem for many years. The same problem for both animal and biologist afflicts fishes that hold position in murky, moving water (Howland and Howland 1962).

7. Swimming

Swimming while fully submerged, as is usual among animals, involves the same general trade-offs and opportunities as does flying. Still, as a more forgiving locomotory mode, it affords a wider range of designs and solutions. Per unit distance covered it costs less than flying or any terrestrial gait. Per unit time – since hovering costs next to nothing – it costs far less even than any form of active flying. Only soaring, essentially gravity-sustained, can come close. While economical, though, the same cost-benefit calculation applies to both predators and prey; and suspension feeders

that actively swim (or pump) face the outcome of success by all other and previous suspension feeders. So once again we encounter systems balancing stability, maneuverability, and efficient performance. Again, maneuverability typically comes at a price in reduced locomotor efficiency.

Most swimming vertebrates do have a particular non-locomotory instability with little parallel among fliers. Achieving buoyancy with a non-rigid gas-filled container makes them unstable with respect to depth. Thus increased depth compresses the gas, reduces buoyancy, and impels an animal to go still deeper. The problem and its various solutions formed a large part of essay 8 (Vogel 2006b).

That gas bladder contributes to a more subtle problem. If the center of the water displaced by a submerged object lies below the center of gravity, then the object would prefer to be inverted. With the usual convention, the vertical distance between the centers, the so called “metacentric height,” is negative. Although the bladder has moved from its ancestral ventral location (like lungs) to a position above the gut, bony fish with swimbladders usually still have negative metacentric heights, giving them unstable normal postures – a dead fish ordinarily goes belly up. Fish that live in moving streams seem to be the most unstable, perhaps because they have to expend power continuously to hold position anyway. Fish that live in still water and do not swim continuously tend to be less unstable. In addition to making “resting” easier, a stationary fish cannot trim a hydrodynamic surface to adjust position and thus lacks that mode of active stabilization (Webb 2002.)

In general, both fish and cetaceans have considerable instability as a result of their motion through water. The situation resembles what we saw for flying animals in that stability and maneuverability are again to a considerable extent antithetical. That speed trades off against maneuverability appears even clearer for the swimmers than for flyers. And stiff bodied forms tend to be both faster and less maneuverable than flexible ones, whether one compares cetaceans (Fish 2002) or fishes (Webb 2002).

Swimmers most often propel themselves with driving devices at their downstream ends, whether the fins of fishes, the flukes of cetaceans or the jets of cephalopods. (But not always – some fish use pectoral fins or opercular jets while penguins, some other birds, and sea lions, to mention a few, use modified forelimbs.) Pushing from behind rather than pulling from in front generates an additional mode of instability. Any inadvertent yaw means that one component of the output of the propulsor will give rise to a turning moment that will amplify the initial yaw. Still, it does not appear to create any noteworthy difficulty despite the analogous instability of rear-propelled, rear-heavy automobiles and the instability of pushes that (except in jet-propelled forms) alternate from one side of the body to the other.

Another form of instability comes from trimming controls in front of centers of gravity. Hammerhead sharks, as noted earlier, may use the hammerhead as a canard wing, a seriously destabilizing device, to gain maneuverability that helps follow at a fixed distance above a non-level substratum. And skates and rays may be doing the same with their relatively anterior “wings” – many species do swim just above the substratum, and all of these elasmobranchs have subterminal rather than (as in bony fishes) terminal mouths. Less extreme are ordinary pectoral fins and flippers, but these nonetheless commonly lie ahead of the centers of both buoyancy and gravity in both fishes and cetaceans (Fish 2002).

In both fliers and swimmers, large forms that chase small forms for food tend to be somewhat slower, less stable, and more maneuverable than closely related large forms that have other modes of feeding. The large predator retains a speed advantage but must offset its intrinsically worse minimum turning radius and maximum turning rate. That trade-off appears strikingly in interspecific comparisons among toothed whales (Woodward *et al* 2006). Humpback whales, notably acrobatic baleen whales, have unusually large pectoral flippers and are not especially rapid swimmers (Nowak 1991) by large-whale standards. In dragonflies, large aerial predators, the motor drives the wings directly rather than indirectly, as in most other insects, by which they gain an unusual degree of independence of control of their four wings (D E Alexander 1986).

Swimming at the surface – partly submerged – encounters a particularly nasty form of the problem of negative metacentric heights. Floating high in the water virtually guarantees a highly negative value unless the craft contains a lot of ballast located deep in the hull. But the problem can be ameliorated in a way unavailable to the submerged swimmer. Most ships have V-shaped or U-shaped hulls. This geometry requires that the center of gravity of the craft be lifted if it rolls either way from exactly upright, supplying a restoring torque. Counterintuitively, perhaps, a broad, flat bottom with sides that then slope inward yields a craft lacking that region of stability. The few animals that swim at the surface of bodies of water usually do have hulls that taper downward – it is especially conspicuous in young sea turtles (Wyneken, personal communication).

8. The “flights” of non-flyers

All fliers, in the end, achieve stability with aerodynamic devices – adjustable wings, deployable tails, and so forth. Once equipped with propulsive or gliding appendages, the output side of control needs only modest augmentation. But what can a non-flier do if it finds itself in midair and has some incentive to land in a specific orientation? While hydrodynamic control can be effected by fairly small

structures, only the smallest non-fliers can press ordinary appendages into effective aerodynamic service. Thus some ants that live high in tropical forests make stable flying jumps at respectable glide angles (moving abdomen first, incidentally) by orienting their legs to provide aerodynamic stabilization (Yanoviak *et al* 2005). Larger ones must play with angular acceleration and velocity in a world that awkwardly insists that angular momentum be conserved.

Just as the product of mass and linear velocity gives ordinary momentum, the product of moment of inertia, I , and angular velocity, ω , equals angular momentum, H :

$$H = I\omega. \quad (7)$$

And moment of inertia, essentially the second moment of mass, is the summed elements of mass, m , times, for each element, the square of its distance, r , from the axis of rotation:

$$I = \sum mr^2 = \int r^2 dm. \quad (8)$$

Constancy of angular momentum means that angular velocity can be changed only with a concomitant inverse change in moment of inertia. In a world that also believes that mass must be conserved, changing moment of inertia depends on changing the effective overall r , the “radius of gyration.”

Increasing angular velocity by decreasing radius of gyration – a figure skater or ballet dancer does that by drawing arms and legs closer to the torso and thus to the axis of rotation. Alternatively, an external contact can impose a

moment that imparts angular velocity. A springboard diver can do that in at least two ways (Frolich 1979). A run out along the board gives the whole body a translatory velocity, but the jump at the end, besides imparting an upward component to velocity, slows the lower part of the body (figure 7a). So the diver takes off with some angular velocity and angular momentum. Tucking in legs and arms in midair then increases angular velocity; with (as conservation requires) no change in angular momentum, a somersault ensues. Additionally (or with no run-up), the diver may jump with the body tilted forward so the resulting torque of the vertical push imparts an initial angular velocity (figure 7b). Either way, that angular velocity must be minimized again before entering the water by extending arms and legs.

It has sometimes been contended that conservation of angular momentum requires that any mid-air rotation must trace back to an initial, visually subtle, angular velocity. If by “rotation” one implies time-averaged net angular momentum, then the contention (absent aerodynamic or Coriolis effects) must be correct. Less self-evidently, changes in body orientation – rotation about any axis – can be effected without such net change in angular momentum of the body as a whole. Such orientational changes have been unequivocally demonstrated in springboard divers, acrobats, trampoline jumpers, space walkers, and falling cats (as well as some other mammals). Frolich (1979) and Edwards (1986) provide good descriptions and analyses of how it can be done; Brancazio (1984) gives a quick summary, and Stewart (2004) shows a nice set of color photographs of a falling cat.

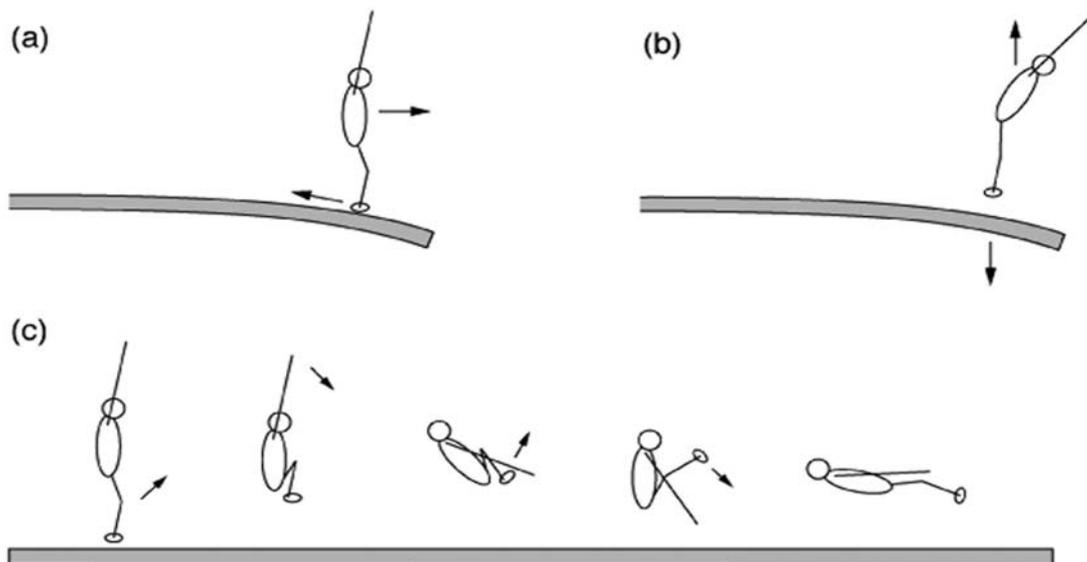


Figure 7. (a) Turning during a springboard dive by making the feet lag the torso. (b) Turning by taking off with head and torso forward of the final contact point. (c) The sequence in which appendages are moved to perform a zero-angular-momentum back quarter somersault, as described by Frolich (1979).

Figure 7c, adapted from Frolich (1979), shows stages of a reorientation about the body's long axis (in pitch) by a diver or gymnast. Initially the body extends full length. Tucking legs up close to the torso reduces the moment of inertia – not in itself inducing much orientational change, but amplifying the subsequent change. Swinging the arms forward and down against the body and thus giving them angular velocity and momentum induces an equal and opposite angular momentum and (of course lesser) velocity of the rest of the body. When the arm motion stops, the motion of the rest of the body has to stop. But the body has shifted orientation substantially – up to about 80°. The arms may then be reextended by moving them along the body axis or swinging them outward to restore the original extended posture. That moment of inertia is a second, rather than a first, moment – incorporating r^2 rather than r – makes even fairly light appendages quite useful, as long as they are reasonably long.

Note a characteristic – and diagnostic – difference between turns that take advantage of initial angular momentum and those that manage despite zero angular momentum. In the first, angular momentum and thus angular velocity remain at the end, so the body keeps rotating unless stopped by some external agency. In the second, the body, having no overall angular momentum, stops as soon as movement of some parts relative to others terminates. One can experience both in a swivel chair. Initial angular momentum just takes push against floor or desk, what one ordinarily does in such a chair. But one can turn, say, counterclockwise, by extending the arms, swinging both clockwise, drawing them back against the torso while moving them counterclockwise, extending them again, and repeating – each time progressing a few degrees. Holding weights in the hands increases the effectiveness of the maneuver. (As an exercise, the reader might now attempt to explain how a child can put a swing in motion.)

Domestic cats, famously able to land on their feet, do just such zero angular momentum turns as they fall. Reportedly, cats can turn 180° around their long axes during a 1-m fall, which takes less than half a second. Peak head acceleration (where the turning begins) has been reported to exceed $120,000\text{ s}^{-2}$ (O'Leary and Ravasio 1994). Tailless cats tail tailed ones in tests. According to Kane and Scher (1969) and Edwards (1986), and as in figure 8, the supine cat begins by arching the back so the whole animal is concave upward. It then twists the body about the vertebral column, beginning with the head, while maintaining that downward concavity, until the whole torso faces downward, and then straightens the back again, halting rotation.

Dogs, less limber, are less adept at righting; in one informal test, a dachshund failed completely, taking umbrage at the imposition. Rats and many other small mammals, though, right themselves quite competently.

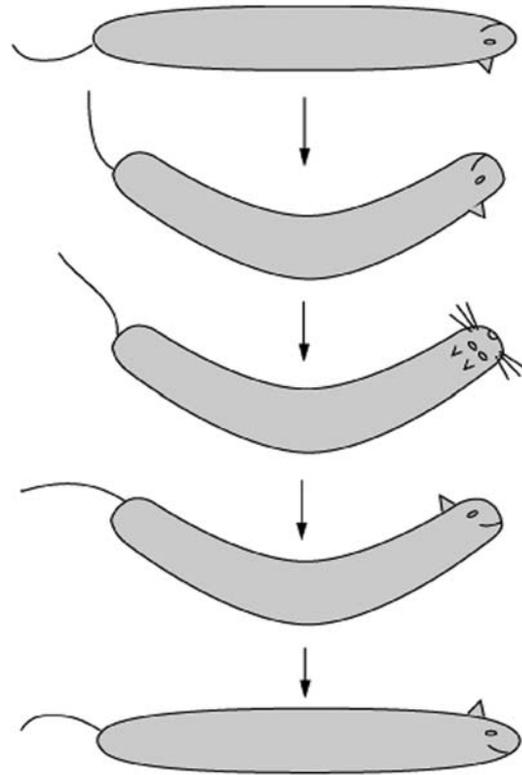


Figure 8. Righting of a mammal's torso with a zero-angular-momentum twist, as explained by Edwards (1986). In practice the twist begins at the head, the tail counterrotates, and movement of the legs (in a manner analogous to that shown in figure 7c) plays at least a supporting role.

The behavior not only ensures landing on properly shock-mounted appendages to lower deceleration, but it also must increase drag during long descents, reducing both terminal velocity and the rate of approach to terminal velocity.

Spinner dolphins (*Stenella longirostris*) make spectacular upward leaps, rotating while airborne as many as seven times about the long axes of their bodies. But, by contrast with cats, they make no significant use of zero angular momentum turning; instead, they drive their aerial turning by asymmetrical motion of their flukes just prior to emersion. The behaviour appears to cause dislodgment of remoras as they reenter the water (Fish *et al* 2006). One might expect that the high drag an animal experiences in water renders inertial turning both ineffective and unnecessary. But we should not dismiss the possibility out of hand. Photographs of the so-called pinwheeling maneuver of bottlenose dolphins (*Tursiops truncatus*) (Maresh *et al* 2004) look to my eyes strikingly similar to photographs and diagrams of righting cats.

We know less about non-mammalian cases of righting with zero angular momentum turns. An unfledged bird falling from a nests probably has sufficient plumage to keep

it from reach a hazardous terminal velocity – the speed at which drag, speed-dependent, reaches weight. And most of the non-flying, non-mammalian gliders such as flying frogs and lizards, can exert aerodynamic control. An exception might be flying snakes (genus *Chrysopelea*), which while gliding downward do quite a lot of mid-air writhing and maneuvering (Socha *et al* 2005).

The relative utility of inertial and aerodynamic mid-air turning depends on both airspeed and body size. Faster motion favors reliance on aerodynamics, with both lift and drag increasing with something close to the square of speed. Larger size favors inertial turning due to the concomitant reduction in surface-to-volume ratio. Humans can, as we have seen, do quite well at inertial turning. But aerodynamic effects should not be casually dismissed since large animals fall somewhat more rapidly than small ones. Moreover, significant use of inertial turning has recently been demonstrated (along with aerodynamic turning) in flying birds (Hedrich *et al* 2007). Most birds perform downstrokes with extended wings and upstrokes with somewhat flexed wings. Flying straight generates no overall difference in moment of inertia since the two wings cancel each other's asymmetry. But when turning, the outer wing increases amplitude, which will roll that side upward, aiding the extra aerodynamic lift but without extracting a price in drag.

One odd convergence in small mammals suggests routine use of aerodynamic turning. In at least four lineages, long-hind-legged jumping animals have long tails (longer than head + body) with tufts of hair on their ends. Three of these are rodents – kangaroo rats (*Dipodomys*; Heteromyidae), some gerbils and jirds (*Gerbillurus*, *Meriones*; Muridae); and jerboas (*Dipus*, *Jaculus*, etc; Dipodidae). One is a marsupial – the kultarr (*Antechinomys*). Comparably long-tailed animals without long hind legs typically lack such terminal tufts, judging from the photographs in Nowak (1991). Movies of kangaroo rats engaged in intraspecific interactions show extended tails flung vigorously in all directions, with the tufts clearly visible. (See, for instance Disney 1953.) Still photographs taken under comparable circumstances often show erected tail hairs (Schmidt-Nielsen, personal observation). Perhaps the tuft, especially when erected, increases the drag of a tail moved laterally, and drag so far from the body provides torque that aids turning of the body in the other direction. Thus aerodynamic and inertial devices might combine in aiding mid-air maneuvering – but I am not aware that the phenomenon has been investigated.

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