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Commentary

Paradox lost: answers and questions about walking on water

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Summary

The mechanism by which surface tension allows water striders (members of the genus *Gerris*) to stand on the surface of a pond or stream is a classic example for introductory classes in animal mechanics. Until recently, however, the question of how these insects propelled themselves remained open. One plausible mechanism – creating momentum in the water *via* the production of capillary waves – led to a paradox: juvenile water striders move their limbs too slowly to produce waves, but nonetheless travel across the water's surface. Two recent papers demonstrate that both water striders and water-walking spiders circumvent this paradox by foregoing any reliance on waves to gain purchase on the water. Instead they use their legs as oars, and the capillary 'dimple' formed by each leg acts as the oar's blade. The resulting hydrodynamic drag produces vortices in the water, and the motion of these vortices imparts the necessary fluid momentum. These studies pave the way for a more thorough understanding of the complex mechanics of walking on water, and an exploration of how this intriguing form of locomotion scales with the size of the organism.

Key words: *Gerris*, water strider, capillary wave, Denny's paradox, spider.

Introduction

There is something intrinsically fascinating about organisms that move differently than we do. It has been 30 years since my first course in animal flight, but the sight of a hummingbird hovering before a flower still causes me to stop and stare. Salmon leaping, snails crawling, jellyfish pulsing – when faced with the incredible variation in animal locomotion, one can't help but gaze and wonder: how do they do that? In most cases, an answer (or at least a plausible theory) is readily available, and two recent book-length overviews (Alexander, 2003; Biewener, 2003) go far toward scratching one's intellectual itch. All the more fun, then, when the answer to the question of 'how do they do that?' is that no one knows. Until recently that was the situation with insects and spiders that walk on water.

The fascination here is actually twofold. Before one can understand how a water strider can move about, one has first to explain how they can even stand on the water's surface. In this case, the explanation is well known. First, the attraction of one water molecule to another requires that considerable energy be expended to create new area of air–water interface. Pure water has a surface energy of approximately 0.07 J m^{-2} (Denny, 1993). Now, surface energy (J m^{-2}) is dimensionally equivalent to a capillary tension (N m^{-1}), and it is in this disguise that it will be employed here. Second, when a hydrophobic object is pressed into the interface between air and water, the water attempts to minimize its contact with the object, often at the expense of creating new surface area. As a result, when a water strider presses one of its hydrophobic legs down onto the surface of a pond, a dimple is formed in the water's surface, and the surface is stretched (Fig. 1). The vertical component of the resulting capillary force resists the downward push of the leg (Fig. 2), and the water strider is supported (e.g. Vogel, 1988; Denny, 1993).

This explanation leads to a classic example of biological scaling. The capillary force that supports a water strider is proportional to the perimeter of the legs in contact with the liquid, and therefore scales roughly in proportion to some linear dimension of the organism. In contrast, the weight of the animal (the force pushing the legs downward) is proportional to the animal's volume, and therefore approximately to the cube of its linear dimension. In other words, with an increase in size, the tendency to sink into the water increases much more rapidly than the ability to resist. As a consequence, standing on water is a knack confined to small organisms. Hu et al. (2003) show that large water striders have disproportionately longer legs, allowing these insects to reach somewhat larger sizes than we might expect. But the allometric change in leg length is not sufficient to completely offset the drastic increase in mass, and water striders are, indeed, confined to small body size.

This scaling argument has long been standard fare in introductory biology classes, but in my experience, its

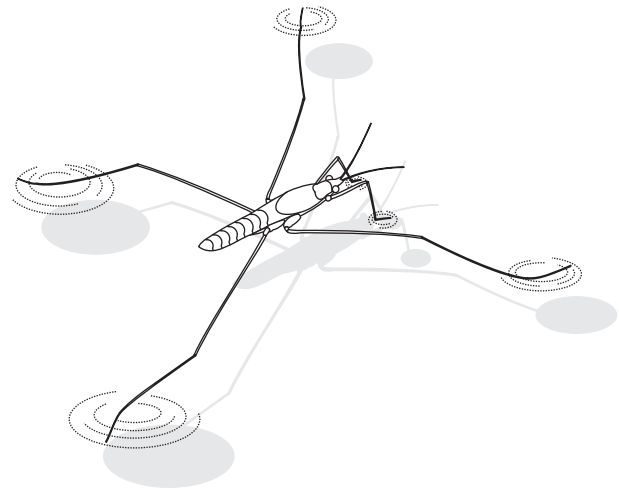

Fig. 1. A water strider standing motionless on the water's surface. Note the dimples where the feet contact the water.

presentation is immediately followed by a pertinent question. Granted, small insects and spiders can stand on water, but how do they move about? Early attempts at an answer led to an apparent paradox.

Denny's paradox

The problem, at least, is intuitive. If a water strider, initially still, begins to move across the surface of a pond, it gains some momentum. It can do so only by imparting an equal and oppositely directed momentum to it surroundings, either the air or the water. Because the density of air is so small, it seems most likely that the insect moves by somehow creating momentum in the water. This process is familiar to anyone who has rowed a boat. The mass of the boat is propelled forward by the backward-directed momentum of water pushed by the oars. The question, then, is how does the insect push on the water?

It was at this point that the scientific study of water-strider locomotion initially went astray. When faced with a basic question in locomotion, it is often best to start by filming the animal as it moves. Water striders can be brought into the laboratory, where they busily dart about on the surface of water in a shallow tray, and when lit with bright lights, their motion is readily photographed. The most strikingly apparent aspect of these photographs is the pattern of waves that is produced each time an adult strider moves, waves that move in the opposite direction from the insect. Could the momentum associated with these waves be the momentum required for locomotion?

The idea has a certain appeal. The relatively large water waves with which we are most familiar propagate as a result of the inertial interaction between the water's mass and the restoring force of gravity. In contrast, waves with the short wavelengths produced by water striders (capillary waves) move in part as a result of the interaction between mass and surface tension. Wouldn't it be lovely if the same property of water that accounted for the water striders' ability to stand (surface tension), could also account for their ability to move?

There is a problem, however. As the wavelength, λ, of a pure capillary wave increases, the speed of the wave, c_c, slows down (see Denny, 1993):

$$c_c = \sqrt{\frac{2\pi\gamma}{\rho\lambda}}\,. \tag{1}$$

Here γ is the surface tension of the air–water interface and ρ is the water's density (approximately 1000 kg m^{-3}). In contrast, the speed of a pure gravity wave, c_g, increases with an increase in wavelength:

$$c_g = \sqrt{\frac{\boldsymbol{g}\lambda}{2\pi}}\,, \tag{2}$$

where $\boldsymbol{g}$ is the acceleration of gravity, 9.81 m s^{-2}. In reality, the speed of a surface wave is a combination of these characteristics:

$$c = \sqrt{\frac{2\pi\gamma}{\rho\lambda} + \frac{\boldsymbol{g}\lambda}{2\pi}}\,. \tag{3}$$

The net result of the combined influences of gravity and surface tension is that there is a minimum speed at which waves can move on the surface of a liquid (Fig. 3). Taking the derivative of Eq. 3 with respect to wavelength and setting it equal to zero, we find that the wavelength at minimum speed is:

$$\lambda_{min} = 2\pi\sqrt{\frac{\gamma}{\rho\boldsymbol{g}}}\,. \tag{4}$$

Inserting this value into Eq. 3, yields the minimum wave speed:

$$c_{min} = \sqrt[4]{\frac{4\boldsymbol{g}\gamma}{\rho}}\,. \tag{5}$$

For an air–water interface, this minimum speed is approximately 23 cm s^{-1}. Now, in order to produce a surface

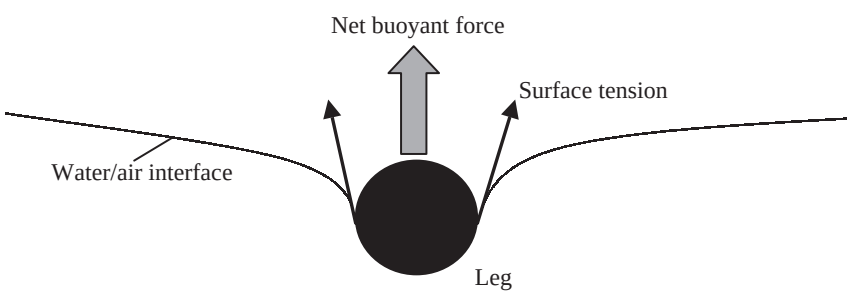

Fig. 2. Surface tension (which acts parallel to the air–water interface) pulls upward on the leg of a water strider.

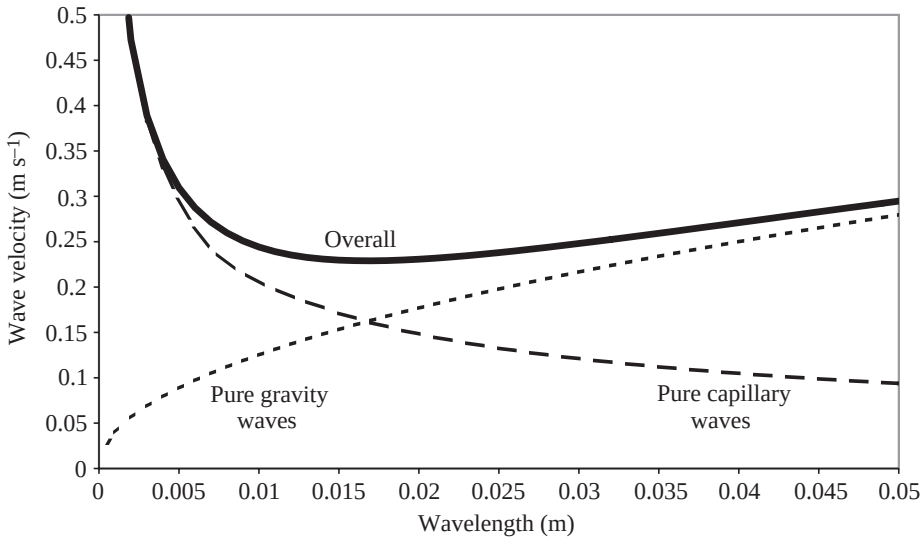

Fig. 3. The speed of a pure capillary wave decreases with an increase in wavelength, while the speed of a pure gravity wave increases with an increase in wavelength. For real waves, the result is a minimum wave speed.

wave, the object responsible must be moving at least as fast as the wave it creates. Thus, the minimum speed of surface waves sets a minimum speed at which the leg of a water strider must move in order to make waves.

Therein lies the problem. 23 cm s^{-1} is a relatively high speed for the leg of a small insect. For example, the middle leg of a juvenile water strider may be only 2 mm long. In order for the tip of this leg to move at 23 cm s^{-1}, the leg must swing with an angular velocity of 115 rad s^{-1}. The entire propulsive stroke (which involves a rotation of about 1.5 rad) must therefore occur in about 13 ms. If the leg can't rotate that fast, it can't produce waves. And if waves are the only means by which it can impart momentum to the fluid, the inability to move the legs at 23 cm s^{-1} means that the animal can't move about.

Indeed, juvenile water striders do not swing the tips of their legs at 23 cm s^{-1}, and they do not produce waves. They do, however, scamper over the water's surface just fine. This disparity between locomotory theory and organismal reality (noted by briefly in Denny, 1993) became known as 'Denny's paradox' (Suter et al., 1997; Hu et al., 2003).

The role of a paradox

Paradoxes in locomotion have often been the impetus for valuable research. For example, in 1936, based on theory and measurements then available, Sir James Gray calculated that the power a dolphin would expend to overcome hydrodynamic drag was considerably greater than the power available from its muscles. 'Gray's paradox' spurred decades of research on both the reduction of drag by the damping of turbulent fluctuations and the energetics of mammalian muscle. The current thought is that dolphins and whales have somewhat less drag than Gray supposed, and that their muscles produce substantially more power. As our understanding improved, Gray's paradox faded away, and it is not even mentioned in recent texts (e.g. Alexander, 2003). Similarly, an engineer, André Sainte-Laguë, used steady-state aerodynamic theory to calculate that bumble bees should not be able to fly (Magnan, 1934). Aside from making engineers the butt of jokes among several generations of science writers (see Dickinson, 2001), the 'bumblebee paradox' served as a starting point for the recent revolution in our understanding of insect flight. Steady-state aerodynamics indeed cannot explain how a bumblebee flies (Ellington, 1984); an understanding of the complexities of small-scale, unsteady aerodynamics is necessary (e.g. Ellington et al., 1996; Dickinson et al., 2000).

Paradox solved

Although not in the same league as Gray's paradox or the bumblebee paradox, Denny's paradox nonetheless tweaked the curiosity of a variety of scientists and engineers, and recent work suggests that it has been solved. The initial breakthrough came with a study not of water striders (the organism in which the paradox was framed), but rather of an oddball spider that walks on water. Suter et al. (1997) glued the leg of the fisher spider *Diomedes triton* to a sensitive drag transducer, and with the leg in its natural posture brought its tip into contact with the surface of a smoothly flowing surface of water. Even though the speed of the water was less than 23 cm s^{-1} and no waves were produced, the leg encountered substantial drag. Suter and his coworkers hypothesized that this drag was due not to a surface phenomenon (such as waves), but rather to conventional pressure drag resulting from the pattern of flow around the leg's dimple. By arbitrarily assuming that the drag coefficient of the dimple was half that of a circular cylinder, Suter et al. estimated that the drag on the dimple could account for 60–98% of the overall force on the leg at velocities <0.2 m s^{-1}. Suter et al. thus solved Denny's paradox by clearly demonstrating that surface waves were not the only mechanism by which an organism on the water's surface could create momentum in the water.

The study left several questions unanswered, however.

Although Suter et al. measured a drag force under steady flow, they did not quantify the pattern of flow that was responsible. In particular, their experiments did not allow them to describe what happens as the leg's motion stops at the end of a rowing stoke. Exactly how is momentum imparted to the water? Furthermore, all their measurements were conducted at a flow speed below the critical wave speed. What happens when waves are present?

These questions served as the basis for the recent study by Hu et al. (2003). Through careful use of high-speed video and the presence of dye and particles in the water, Hu et al. showed that the locomotory motion of each rowing leg of the water strider *Gerrus remigis* imparts momentum to the water through the formation of surface waves, but, more importantly, also through the formation of a hemispherical, dipolar vortex. This unusual vortical structure can be visualized as half of a typical toroidal vortex ring in which the ring has been sliced parallel to its axis of symmetry. The 'cut surface' of the torus lies at the water's surface, and each vortex travels in the opposite direction from the water strider at a speed of approximately V=4 cm s^{-1} (Fig. 4)

Having visualized the flow imparted to the water by the strider, Hu et al. easily calculated the associated momentum. Because the vortex is approximately hemispherical, it volume is $\frac{2}{3}\pi R^3$, where R is the radius of the hemisphere (about 4 mm for an adult strider). The mass of each vortex is thus $M_v=\frac{2}{3}\pi\rho R^3$, its momentum is M_vV, and the overall momentum imparted to the water by the two rowing legs is $2M_vV$, approximately 10^{-5} kg m s^{-1}. The strider itself has a mass of approximately 10^{-5} kg and moves at a speed of 1 m s^{-1}, so it, too, has a momentum of 10^{-5} kg m s^{-1}. In other words, even when surface waves are produced (as they are by adult striders) the waves account for at most a negligible fraction of the overall momentum necessary for locomotion. Here, then, is conclusive proof from freely moving animals that Denny's paradox can be circumvented.

In fact, the rowing locomotion of water striders appears to be quite efficient. When an insect of mass M_i moves forward at speed U, it its body has a kinetic energy equal to $\frac{1}{2}M_iU^2$. In terms of the animal's locomotion this is 'useful' energy. In the process of accelerating its body, however, the strider does work on the water. To a first approximation, this 'wasted' energy is M_vV^2 (that is, half the mass of a vortex times the square of its velocity for each of the two vortices). This information can be used to construct an index of the hydrodynamic efficiency of this form of locomotion:

$$\text{Efficiency} = \frac{\text{Useful energy}}{\text{Useful + Wasted energy}} = \frac{\frac{1}{2}M_iU^2}{\frac{1}{2}M_iU^2 + M_vV^2}. \quad (6)$$

A water strider with a mass of 0.01 g moves forward at 100 cm s^{-1} after producing vortices with a radius of 4 mm that move backwards at a velocity of 4 cm s^{-1}. Inserting these values into Eq. 6, we find that the efficiency of this rowing stroke is about 96%! By utilizing vortices to propel a large volume of water backwards at a low speed, water striders create a large amount of momentum with the expenditure of little work.

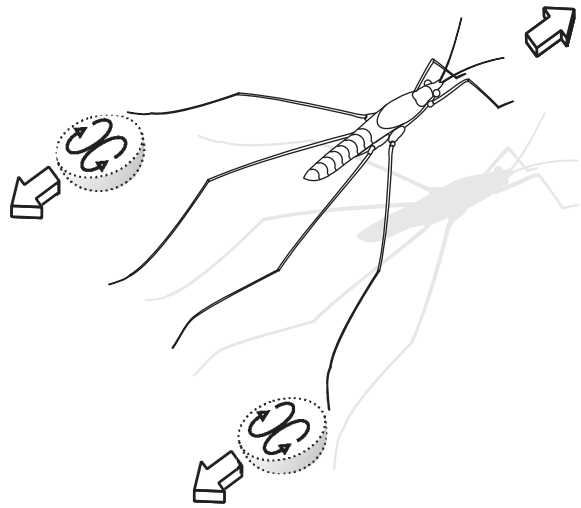

Fig. 4. As a water strider sweeps its middle legs backward, momentum is produced in the water associated with hemispherical vortices.

Open questions

As with most ground- (or water-)breaking studies, those of Suter et al. (1997) and Hu et al. (2003) lead to further questions. It is now clear that water striders and aquatic spiders can row themselves over the water using their legs as oar shafts and the dimples in the water's surface as the oars' blades. But the shape of these blades is extremely dynamic. As a leg moves backward, the shape of the dimple adjusts to the instantaneous force placed upon it both by the leg and by the flow relative to the dimple. Whereas the shape of the static dimple can be described accurately (see, for example, Princen, 1969), I know of no attempt to account for the complex interaction among surface tension, fluid momentum, viscosity and pressure that must take place in the moving dimple. Without at least a description of how the shape of the dimple changes through the power stroke, it is unlikely that we will be able to account for the precise manner in which vortices are produced.

There is also a potential problem associated with surface tension itself. For example, the dimple of a water strider's leg moving at a steady velocity is akin to a bubble rising through a liquid (beer, for example). In both cases, the pattern of flow in the liquid is due to the motion of an air–water interface. Fluid dynamicists have long realized that this type of motion is unusual in that, unlike motion relative to a solid object, fluid motion relative to an air–water interface allows for slippage of water at the interface itself. For example, the theoretical drag coefficient of a small air bubble rising in water is only 2/3 that of a buoyant sphere made from a solid material (Happel and Brenner, 1973), and slippage at the air–water interface may help to explain why the apparent drag coefficient measured by Suter et al. (1997) is lower than might be expected. Furthermore, there can be discrepancies between the theoretical drag coefficient for a bubble and that measured in an actual fluid. Small bubbles rising in beer move slower than simple theory predicts; instead, they act as if the air–water interface has some 'stiffness'

(Happel and Brenner, 1973). The apparent solidity of the bubble's surface may be due to surface-active agents in the interface. As these molecules are swept back by the flow, they can accumulate at the downstream end of the bubble, and thereby resist slippage in much the same fashion as the surface of a solid. One supposes that surface-active molecules might accumulate along the surface upstream of a water strider's leg, thereby affecting the flow. Alternatively, in 1913 Boussinesq (as cited in Happel and Brenner, 1973) pointed out that surface tension is a static property of a fluid, and therefore it may be inappropriate to use it to explain dynamic processes such as flow around a bubble or dimple. Building on this thought, Boussinesq explained the anomalous motion of small bubbles by hypothesizing that under nonsteady flow (and even in the absence of surface-active molecules), an air–water interface can exhibit an intrinsic elasticity. I should note that bubbles rising in beer are smaller than the leg dimples of water striders and move at a substantially slower speed [that is, they have a lower Reynolds number (see below)], but the issue of slippage at the air–water interface and the possibility of surface elasticity may nonetheless have important consequences for any attempt to precisely model the drag acting on the leg of a water strider or spider.

There is also much to be learned about the scaling of surface locomotion. Hu et al. (2003) note that in order for vortices to be shed from the leg of a water strider, the Reynolds number of the dimple must be greater than approximately 100. As suggested by Hu et al., one can calculate Reynolds number using L, the length of the distal segment of the leg (the tarsus), as an estimate of the flow-wise dimension of the dimple:

$$Re = \frac{uL}{\nu}. \tag{7}$$

Here u is the speed of the dimple over the water (which we approximate using the velocity of the rowing leg relative to the insect's body) and ν is the kinematic viscosity of water (approximately 10^{-6} m^2 s^{-1} for pure water). If Re >100, the product of tarsus length and leg velocity must therefore exceed approximately 10^{-4} m^2 s^{-1}. Given that smaller bugs are likely to have both smaller legs and slower velocities, this relationship potentially places a severe lower limit on the effective size of water striders. If the animals are too small, they cannot move their legs fast enough to create either vortices or surface waves, and they therefore are unlikely to be able to move. Exactly where this limit occurs depends on the scaling of leg length and angular velocity in surface insects, as well as on a more precise determination of the critical Reynolds number that must be exceeded if vortices are to be shed.

We have seen that surface tension sets a maximal size at which animals can support themselves on water; if they get too big, they sink. Vortex shedding is likely to set the minimal size, a limit that appears to fall just below the size of the smallest juvenile water striders. There are other limitations as well. For example, Suter and Wildman (1999) have shown that *D. triton*, the water-walking spider, changes its gait from a rowing motion (of the same sort used by water striders) to a galloping motion as its speed increases. They propose that the change in gait occurs when the rowing legs exceed the speed at which surface tension can maintain the integrity of the surface dimple. Above this critical speed, the legs are stabbed vertically into the water, incurring no appreciable dimple, and the legs subsequently act as simple oars, relying on the drag of the leg alone.

To fully understand this gait transition, we again need to be able to account for the complex dynamics of the leg's surface dimple, and precise answers are therefore unavailable. We can, however, make a rough guess as to the critical speed. Batchelor (1967) suggests that bubbles rising in a liquid begin to deform from their spherical shape if the dynamic pressure of the flow ($\frac{1}{2}\rho u^2$) is a substantial fraction of the pressure increase that surface tension imposes across the air–water interface. In turn, the magnitude of the pressure increase is inversely related to the local curvature of the interface, which, unfortunately, we do not know for the dynamic dimple of a moving water strider. For the sake of argument, let us assume that the radius of curvature of the dimple is approximately equal to r, the radius of the tarsus. The resulting surface-tension-induced pressure is γ/r (Denny, 1993). For a tarsus 1 mm in radius (such as that of the spiders used by Suter and Wildman, 1999), this implies that the dynamic pressure is equal to the surface-tension-induced pressure at a velocity of 38 cm s^{-1}. We might therefore expect that the dimple will become unstable at velocities somewhat slower than this. Indeed, Suter and Wildman (1999) showed that the maximum leg-tip velocity in a rowing spider was about 30 cm s^{-1}. Water striders have tarsi with smaller radii (approximately 40 μm), implying that their legs must move at 191 cm s^{-1} before the dynamic pressure is equal to the surface-tension pressure. Hu et al. (2003) recorded leg velocities of 100 cm s^{-1} with no evidence that the dimple had become unstable.

So, one more locomotory paradox bites the dust, but interesting questions remain before the question of 'how do they do that?' is fully resolved. For the time being, my curiosity will continue to itch.

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