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PREDATOR AVOIDANCE ON THE WATER SURFACE? KINEMATICS AND EFFICACY OF VERTICAL JUMPING BY *DOLOMEDES* (ARANEAE, PISAURIDAE)

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ABSTRACT. Vertical jumps of fishing spiders (*Dolomedes* sp.) from the water surface have been presumed to be evasive behaviors directed against predatory fish. We used high-speed videography to analyze the jumps of fishing spiders and then constructed a numerical model to assess the effectiveness of these jumps in evading predatory strikes by trout. Jump height (mean = 3.7 cm) and duration (mean = 0.17 sec) were similar across spider masses (0.05–0.66 g) but latency to jump increased significantly with mass. To accomplish jumps of similar height, more massive spiders had to generate more force during the propulsive phase of the jump than did smaller spiders; and the contribution of fluid drag to the total force used in jumping was substantially greater for large spiders than for smaller ones. Our model juxtaposing the jumps of spiders and the attacks of trout revealed that jump heights and durations were inadequate: only the most lethargic strikes by trout could be successfully evaded by jumping vertically from the water surface.

Keywords: Hydrodynamics, aquatic locomotion, predation, spider, *Dolomedes*

Fishing spiders (*Dolomedes* sp.; Araneae, Pisauridae), noted for their locomotion on the water surface (e.g., Barnes & Barth 1991; Shultz 1987), are adept at predation both on land and on the surface of ponds and slowly flowing streams (Gorb & Barth 1994). While on the water surface, they can also become prey, captured not only by animals that detect them from above (e.g., frogs, birds) but also by submerged predators (fish). One of the best studied of the fishing spiders, *D. triton* (Walckenaer 1837), has two well-known responses to danger from above: it either disappears under the water surface by climbing downward on submerged vegetation (McAlister 1959; pers. obs.) or it rapidly gallops away across the water surface (Suter & Wildman 1999; Gorb & Barth 1994). We and others (G. Miller, pers. comm.; Suter 1999) have observed that, when startled by sudden water-borne vibrations while at rest on the water surface, these spiders jump vertically and then either gallop away or return to rest. Our working assumption is that the jump functions to decrease the probability of capture by fish. Is this a reasonable assumption?

At first glance, a vertical jump from the water surface would seem to be ineffective as evasive behavior because the spider would land exactly where it started, presumably exactly where the attacking fish had aimed (Fig. 1). But fish (e.g., trout, *Oncorhynchus* spp.) accelerate rapidly when lunging at prey (Domenici & Blake 1997), and rarely do so from directly below their intended victims. Thus an attacking fish usually has a non-vertical trajectory, and a vertical jump by a spider would be effectively evasive if it began in time, were high enough, and were of long enough duration.

The height and duration of a jump, closely linked to each other by the physics of gravitation, depend upon the acceleration the spider can impart to itself by pushing down against the substrate (water, in this case). In earlier studies (Suter et al. 1997; Suter 1999; Suter & Wildman 1999) our laboratory established that the locomotion of fishing spiders on the water surface is based on fluid drag: during horizontal rowing, for example, the dimples in the water surface (caused by the downward push of the spider's hydrophobic legs) move backward as the spider strokes, encounter resistance due to drag, and thereby impart a forward acceleration to the spider. In the current study, we looked closely at the forces involved in jumping because, as with rowing, the forces generated by the interactions of spi-

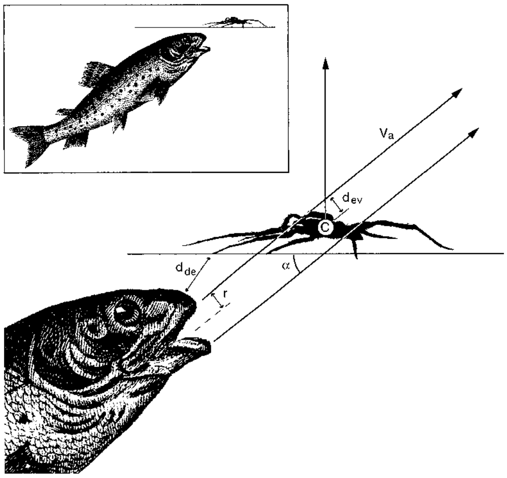

Figure 1.—Diagram of the evasion model. See text for explanation.

der motions and water ultimately govern the qualities of a jump.

METHODS

Spiders.—*Dolomedes triton* are found throughout temperate North America where they inhabit the edges of ponds and slowly flowing streams (Gertsch 1979). The subjects for this study were collected from small ponds in Mississippi and were held in our laboratory under conditions described elsewhere (Suter et al. 1997). Voucher specimens are deposited with the Mississippi Entomological Museum at Mississippi State University. All observations and experiments were conducted at laboratory temperatures between 20–23 °C during local daylight hours.

Kinematics of jumping.—The arena for our studies was a 38 liter aquarium filled to a depth of approximately 4 cm with distilled water. In a trial, we placed the test spider in the arena and used a slender glass rod or gentle puffs of air to maneuver the animal into the center of the arena. At that position its body was at the point of sharpest focus of either a high-speed video camera (Kodak model EktaPro EM-1000) or a 35 mm single lens reflex still camera (Nikon N70). We elicited a jump by sharply hitting the table that supported the aquarium at a distance approximately 2 cm from one corner of the aquarium (approximately 0.3 m from the spider).

The images from the high-speed video were collected at 1000 images per second and stored in S-VHS format (Sony model 9500 MDR). We analyzed the spider's motion in the vertical plane by displaying each digitally-paused video frame on top of a computer-generated x-y cursor grid (NIH Image software, version 1.55 f) by means of a video scan converter (Digital Vision, Inc., model TelevEyes/Pro, connected to an Apple Corporation computer, Power Macintosh 7100/80AV). We then manually digitized the coordinates of the body's approximate center of mass (midway between the top and the bottom of the posterior margin of the cephalothorax) every 5 ms for the duration of a jump, and used the coordinates to calculate the displacement of the spider through time; velocity was calculated for each 5 ms interval. We selected several trials on which we used the same techniques to digitize the locations of the tips of the legs nearest to the camera.

To measure latency, the time between delivery of the stimulus and the first jumping movements, we placed a 2 × 3 cm mirror in the frame of view of the camera and angled it so that the high-speed video would show both the production of the stimulus and the motion of the spider. The vibrations caused by the stimulus could have reached the spider via transmission through about 0.28 m of water (assuming it propagated from the corner of the aquarium) or through only 4 cm of water (assuming it propagated first along the glass base of the aquarium and then vertically through the water directly below the spider. In either case, the vibratory stimulus would have reached the spider in < 0.2 ms (given a transmission velocity of 1497 m/s in distilled water; Weast 1985).

To make still photographs (35mm) of spiders during jumps, we used a percussion sensor and an electronic short-interval timer (LPA Design, LPA Time Machine) to trigger an electronic flash (Vivitar, 285HV) after a known post-stimulus delay.

Calculation of vertical forces.—We used two methods to calculate the vertical forces produced by spiders during jumping. First (the ‘‘acceleration method’’), we calculated average force production by applying Newton's second law ($F = ma$) to our data on spider mass and acceleration (above). Second (the ‘‘leg-motion method’’), analyses of the kinematics of jumping gave us information about the dynamics of the sub-surface portion of the legs. We assumed that, although the sub-surface portion of a leg was not entirely surrounded by water, its motion through the water created a drag force identical to that created by a fully submerged leg segment of the same length and moving at the same average velocity. This is a plausible assumption for two reasons. First, the drag on a submerged cylinder is proportional to the frontal surface area (Denny 1993). And second, our earlier work (Suter & Wildman 1999) showed that Denny's equation for drag on a submerged cylinder, which incorporates both drag coefficients and Reynolds numbers (equation 4.29 in Denny 1993), fit the force data for the legs of spiders galloping across the water. We used Denny's equation to calculate the total thrust force exerted by that leg segment in a direction perpendicular to the leg's long axis, and used trigonometry to resolve that vector into its horizontal and vertical components. For this study, the horizontal component was ignored because the horizontal forces generated by opposing legs (e.g., left I *vs.* right IV) are approximately equal in magnitude and opposite in direction (hence the verticality of the jump).

Evasion model.—The premise underlying our evasion model was that an attack by a fish could be evaded by a fishing spider if the spider's jump occurred at the correct time relative to the attack and if the jump were high enough. In the geometric model (Fig. 1): (a) a fish attacked in a straight line at an angle (α) to the water surface and at a constant velocity (V_α); (b) throughout the attack, the trajectory of the fish was ''aimed'' at the location of the spider at rest on the water surface; that is, the center of the fish's open mouth followed a line that would have, had the spider remained stationary, intersected the center of mass of the spider when the spider was at rest; (c) the spider detected the approach of the fish at a distance (d_{de}, 0–2 cm), using sensors on the part of the spider (body or appendages) nearest to the fish, and began its vertical jump with a latency dictated by data collected in this study; (d) the spider jumped to a height (and with a duration) dictated by data collected in this study; (e) the attacking fish, a trout with attack velocities comparable to published fast start velocities of trout (*Oncorhynchus mykiss*: Domenici & Blake 1997) and with attack angles varying between 20–80°, attacked with its mouth open and circular (radius: r, 1–2 cm); and (f) a successful evasion was defined as one in which the spider's center of gravity was outside of the fish's mouth ($d_{ev} > 0$) at the moment when the center of the mouth crossed the line representing the vertical trajectory of the spider. The attack angle (e, above) was constrained at the lower end by the fact that the spider would be invisible to the fish at angles less than the critical angle of the air-water interface, 48° (Denny 1993); we chose 20° both because we didn't want to underestimate a fish's ability to detect surface distortions even when it could not see through the surface, and because the fish's angle relative to the spider increases as the fish comes close to the spider. At the upper end, the attack angle was constrained by the recognition that, as the angle approaches 90°, a spider jumping vertically could not escape even if its jumps were 3× the highest jumps actually measured.

The model addressed two questions: for what angles of attack (α) and attack velocities (V_α) is spider jumping effective, and how do these parameters compare with actual velocities of attack by fish in the range of angles tested?

RESULTS

Data from high speed videography.—Videography at 1000 images/sec revealed that a jumping *Dolomedes* uses all eight legs, accelerated simultaneously downward, to propel itself into the air above the water surface (Fig. 2). During the propulsive part of the jump, each leg moves so rapidly (angular velocity = 3.36 ± 1.02 degrees/ms; mean ± 1 S.D.) that an air-filled cavity persists behind it throughout the interaction of leg and water (Fig. 3). The peak height that a spider's body reaches during a jump is determined primarily by its velocity at the end of the propulsive part of the jump. That velocity, in turn, is a consequence of the acceleration produced when a force exerted downward by the spider (= upward by the water) moves the mass of the spider. Thus, while the spider is in the air, its center of gravity should follow a parabolic path, decelerated by gravity as the spider rises and accelerated by gravity as the spider falls toward the water. In our study, the spider's paths were nearly perfectly parabolic (Fig. 4), with a characteristic small depression of the

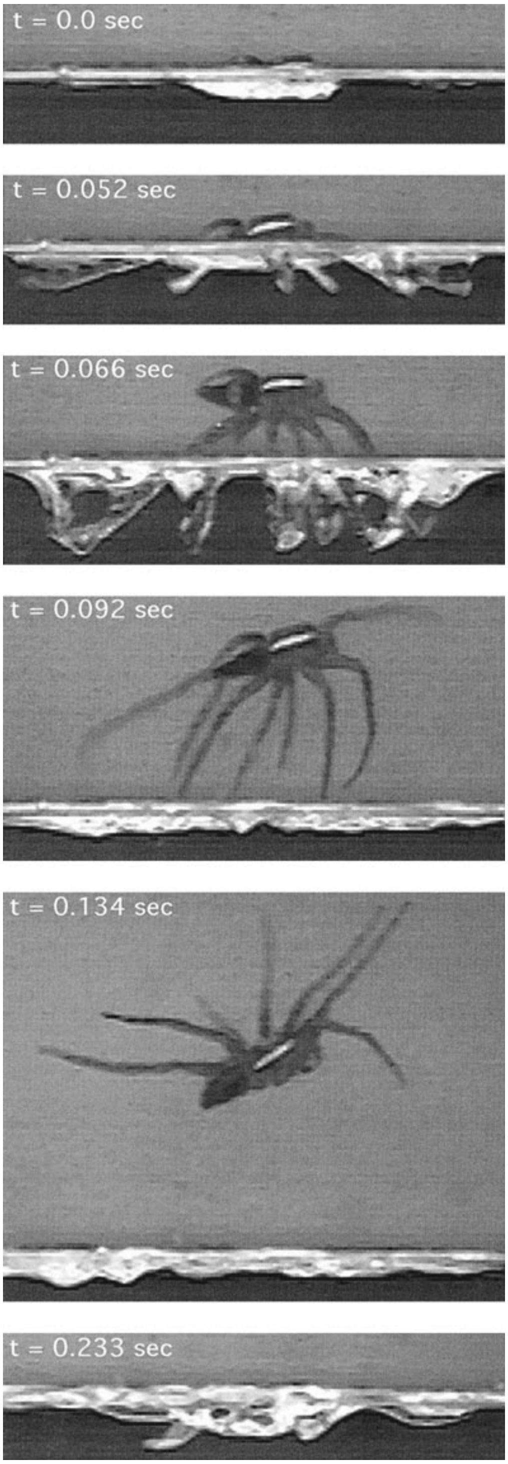

Figure 2.—High-speed lateral views of *Dolomedes* jumping vertically from the water surface. In an analysis of videographic images of a large (0.67 g) female, captured at 1000 frames/sec, the propulsive phase of the jump was completed within the first 90 ms, peak elevation was reached at about 134 ms, and the spider was out of contact with the water for about 141 ms.

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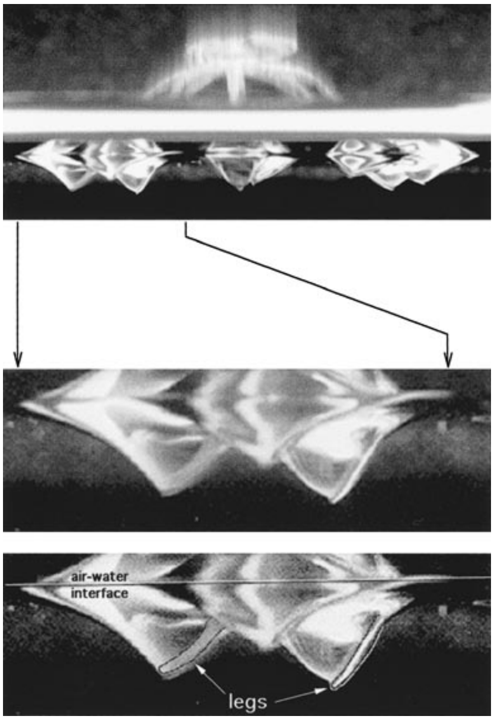

Figure 3.—Details of the sub-surface shapes of cavities formed during the propulsive phase of jumping by a smaller (0.32 g) female are revealed in an image captured on 35 mm film with electronic flash illumination (top). The tips of some tarsi protrude very slightly into the surrounding water. The location of two legs within air-filled cavities can be seen most clearly in the enhanced (bottom) image derived from the enlargement (center).

peak height because the center of gravity of each spider as a whole (legs included) varied with the positions of the legs, and the legs rose and fell relative to the body during a jump (Figs. 2, 4).

The digitization of body height as a function of time (Fig. 5, upper graphs) made it possible to calculate velocity (Δheight/Δtime) and plot velocity as a function of time (Fig. 5, lower graphs). During a jump, we used the downward motion of a leg tip (upper graph, dashed lines) to define the time during which

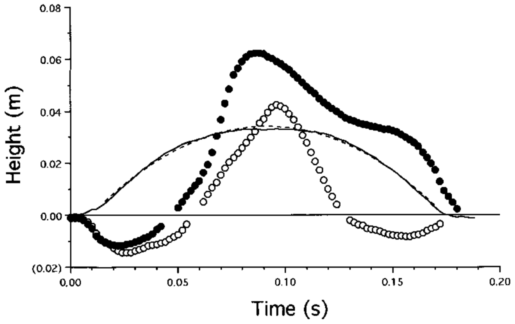

Figure 4.—Digitized tracks of a spider's approximate center of mass (solid line, "—"), the tarsus of a leg I (filled circles, "●"), and the tarsus of a leg IV (open circles, "○"), during a typical vertical jump from the water surface. The trajectory of the spider's center of mass follows nearly perfectly the parabola (dashed line, "—") expected from gravitational mechanics. The sub-surface locations of the tarsi, during the initial 0.06 sec, indicate the propulsive phase of the jump.

propulsive acceleration occurred. For every two adjacent points in these graphs, we calculated the change in height as a function of elapsed time (vertical velocity). Plots of velocity versus time (lower graphs) showed roughly linear accelerations (slopes) for the propulsive and free-fall phases of the jumps: during propulsion, accelerations were rapid, approximately four times the acceleration of gravity; during freefall, calculated accelerations were within 5% of what was expected (9.8 m/s^2) for objects under the influence of gravity alone. In the jump of the larger spider, the steep negative acceleration that occurred between 0.015 and 0.045 sec is the result of the spider's legs rising from below to above its body (see Figs. 2 & 4), causing a rise in the spider's center of mass without a corresponding rise in the position of the spider's body.

Having measured multiple jumps of spiders of five different sizes, we were able to assess performance (i.e., jump height or time in freefall) as a function of mass. A regression of time in freefall on mass (Fig. 6) revealed no

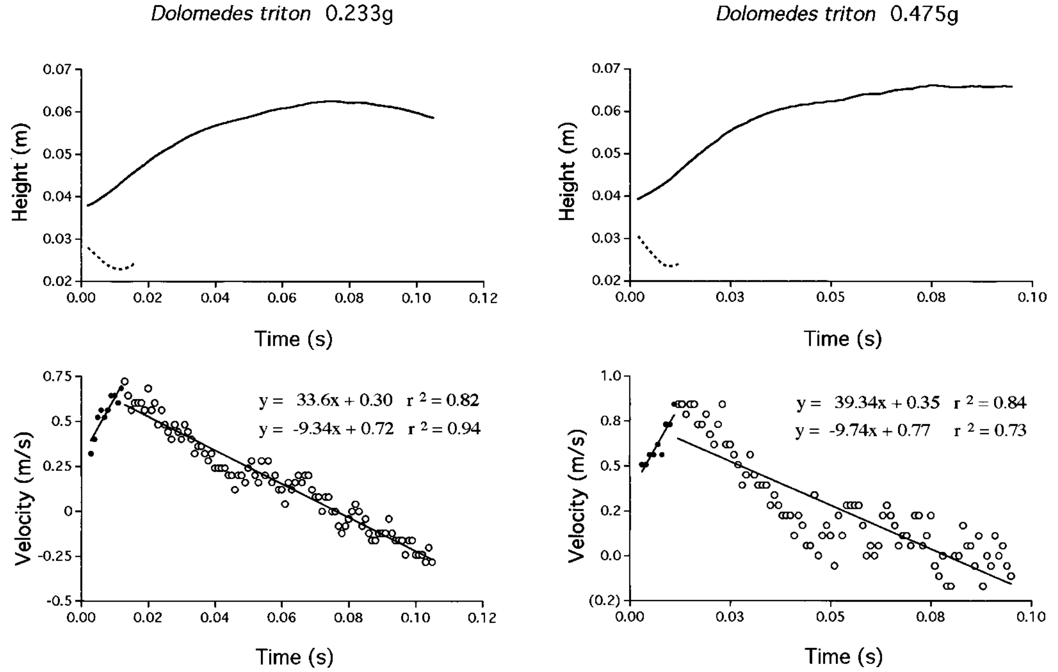

Figure 5.—Calculation of the accelerations due to the propulsive actions of the legs and due to gravity during free-fall. Changes in the height of the spider's center of gravity (upper graphs, solid lines) over time are caused initially by the downward push of the legs (upper graphs, dashed lines) and subsequently by the pull of gravity.

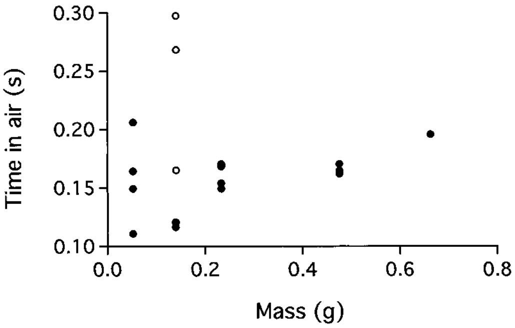

Figure 6.—The mass of a jumping spider does not influence the time the spider spends off of the water surface. The time spent aloft did not vary significantly with mass among females (filled circles, ‘‘●;,’’ $r^2 = 0.21$, $n = 5$, $P > 0.05$; duration $= 0.167 \pm 0.046$ sec, mean ± 1 S.D.) and could not be measured in our data from the single male (open circles, ‘‘○’’).

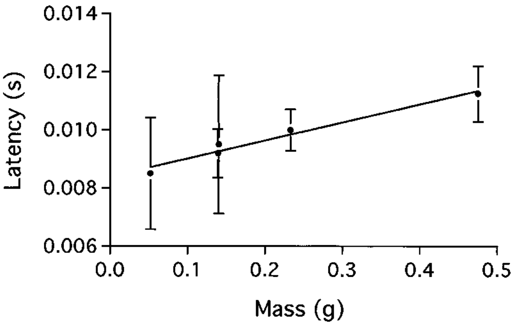

Figure 7.—Latency, the time between the stimulus and the first propulsive motions of the legs, rose significantly with mass (pooled sexes; latency $= 0.006$ mass $+ 0.008$, $r^2 = 0.967$, $n = 5$, $P < 0.01$).

significant relationship. Because time aloft and jump height are physically linked ($h = v_i t - gt^2/2$, where h is height, g is the acceleration of gravity, and t is time in the air), it follows that jump height is also relatively constant across sizes. This result is consistent with allometric measurements of jumping height in terrestrial mammals (Hill 1950; Pennycuick 1992).

Latency to jump (the time between the delivery of the stimulus and the first detectable downward movements of the spider's legs) did vary significantly with spider mass (Fig. 7): the largest spiders we tested were about 33% slower to respond than the smallest.

Because jump height and time in the air were approximately uniform across spider sizes (Fig. 6) and because larger spiders have more mass to accelerate, we assumed that the forces exerted by spiders during jumping would rise linearly with mass. This assumption was confirmed by our measurement of the force/leg used by spiders jumping vertically (Fig. 8, upper graph). The force used to accelerate a spider upward ('acceleration method'') rose significantly with mass (upper graph, solid line: for the pooled sexes, force $= 4.52$ mass $+ 0.039$, $r^2 = 0.970$, $n = 5$, $P < 0.01$).

To investigate the contribution that surface tension may make to the water's resistance to the motion of the legs (and hence the spider's ability to push off from the water surface), we made calculations based upon the following premises: (a) the eight legs contribute equally to the support and vertical propulsion of the spider; (b) about half of each leg is in contact with the water during the propulsive phase of jumping (Fig. 2); (c) leg length is predictably related to spider mass (Suter & Wildman 1999); (d) maximum dimple depth is 3.8 mm (Suter & Wildman 1999).

Our calculations, using vertical forces derived from the ‘‘acceleration method,’’ revealed (Fig. 8, Table 1) that spiders of mass < 0.3 g could become airborne by simply pushing against the resistance caused by the dimples' combination of surface tension and buoyancy (curved, dashed line in Fig. 8, upper graph). Larger spiders, however, had to rely on drag resistance to generate the force necessary to propel them vertically. This difference in the importance of surface tension was also apparent in our force calculations, using vertical forces derived from the ‘‘leg-motion method,’’ concerning the jumps of a 0.05 g spider and a 0.75 g spider (Fig. 8, lower graphs). The vertical component of the force vector produced by the propulsive parts of the legs varied strongly with the angle of each leg relative to horizontal: as a leg approached 90°, the proportion of the force it could generate in a vertical plane approached zero. Not surprisingly, therefore, most of the useful force generation during a jump occurred when the legs were moving fast enough (e.g., not at the very beginning of a downward stroke) and were not at too steep an angle. For the larger of these spiders, the ‘‘submerged’’ portion of

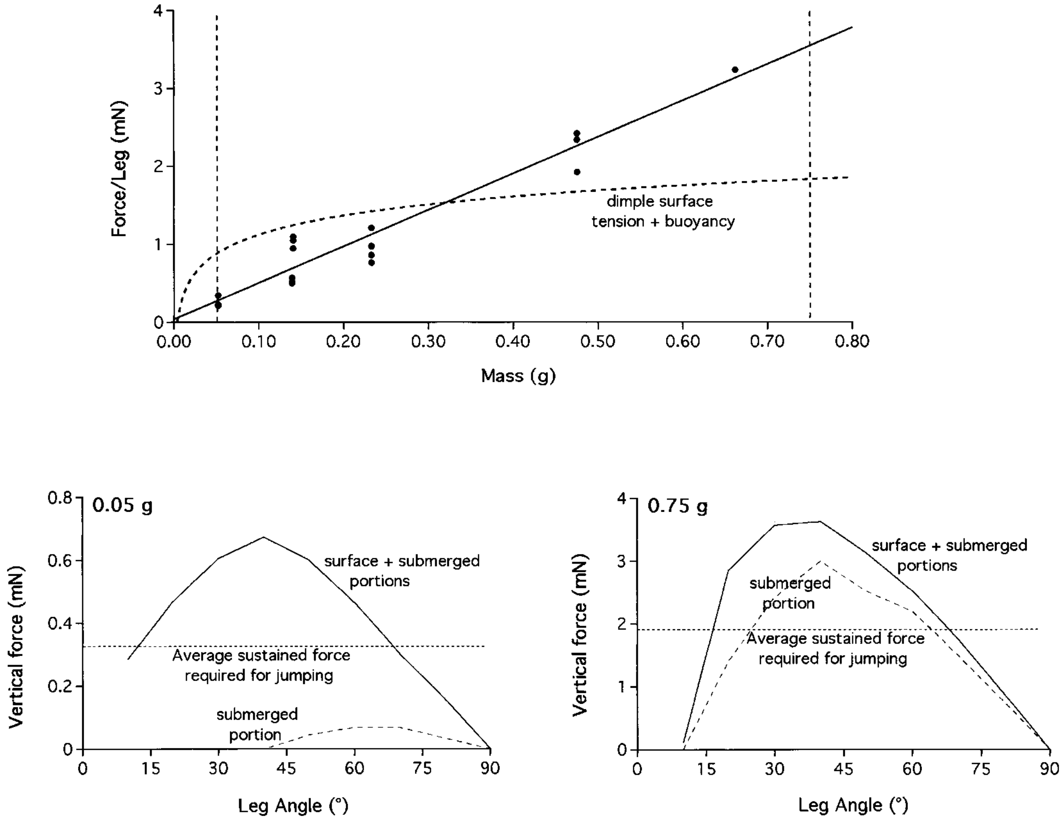

Figure 8.—Upper graph: The force used to accelerate a spider upward (“acceleration method”) rose significantly with mass (solid line, $r^2 = 0.970$, $n = 5$, $P < 0.01$), but only for spiders < 0.3 g was that force available from pushing against the resistance of the dimple (curved, dashed line). Lower graphs: The vertical component of the force vector produced by the propulsive parts of the legs (“leg motion method”) varies strongly with the angle of each leg relative to horizontal. Horizontal dashed lines represent the average force (“acceleration method”) required for a spider of the given mass to perform a jump of average height and duration. Vertical dashed lines in the upper graph mark the masses of the two spiders depicted in the lower graphs.

each leg (the part visible below the water surface in Fig. 3) made a major contribution to vertical force needed for a jump, whereas for the small spider, the submerged portion of the leg made a very small contribution.

Spider jumps in the context of fish strikes.—Our geometrical model (Fig. 1), designed to assess the efficacy of the vertical jump as a fish evasion behavior, combined our data on jump kinematics and latency with published data on trout fast start velocities (Domenici & Blake 1997). In the model, a successful evasion was one in which the spider’s center of mass was outside of the fish’s mouth as the strike trajectory of the fish crossed the jump trajectory of the spider. When we plotted evasion distance (d_{ev}, cm) as a function of the angle of attack (α, degrees) and attack velocity (V_a, m/s), taking all $d_{ev} > 0$ as successful evasions, we found that even large variations in detection distance (0–2 cm) and spider size (0.06–1.0 g) did not render the spider safe at steep angles of attack or at strike velocities > 1 m/s (Fig. 9).

The maximum fast start velocities of trout (Domenici & Blake 1997), averaging 1.66 ± 0.48 (S.D.) m/s, are higher than the strike velocities at which spiders jumping vertically are safe (Fig. 10). Assuming that strikes have approximately the same peak velocities as fast starts, we conclude that only the most lethargic strikes by trout could be evaded by spiders.

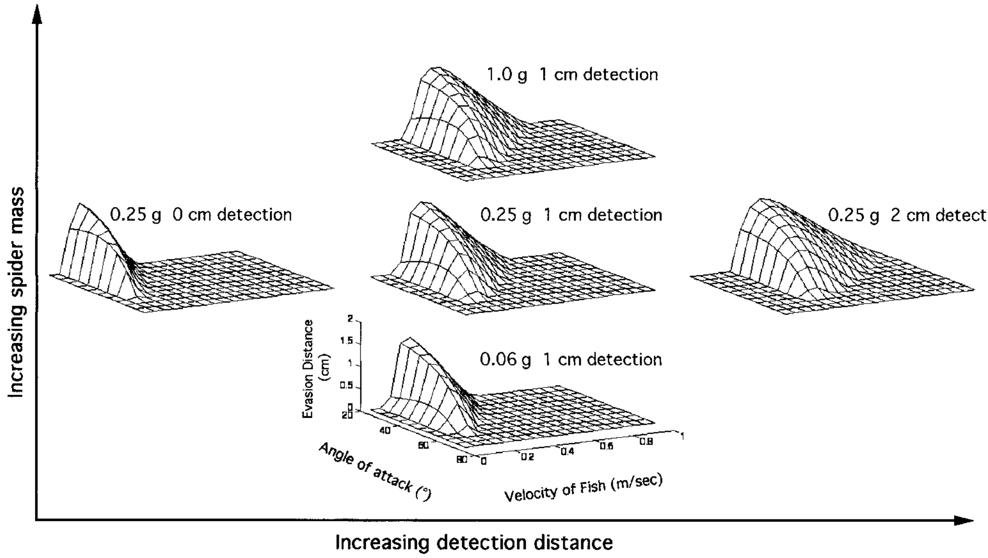

Figure 9.—Success of attack evasion. Evasion was deemed successful if the center of mass of the spider was outside of the trajectory of the trout's mouth as the trout passed through the vertical trajectory of the spider. Thus, all positive values of evasion distance (vertical axis) constitute successful evasions. The evasion distance (d_{ev}, cm) was plotted as zero for negative values of d_{ev} (spider captured) to emphasize the difference between successful evasion and failure. In all situations, the velocity of the attacking fish and its angle of attack strongly influenced the efficacy of evasive jumping. Increases in the distance at which fish attacks could be detected, d_{de}, substantially increased the evasion success footprint, and increases in spider size had a similar effect.

Table 1.—Jumping from the water surface requires an upward force sufficient both to resist the downward pull of gravity and to accelerate the spider upward. Only for small spiders is the resistance offered by a dimple (surface tension plus buoyancy) sufficient for both (compare last two columns). Values in the last four columns are for a single leg and assume that all eight legs participate in vertical propulsion, that about half of each leg provides thrust, and that maximum dimple depth is 3.8 mm. Column 2, from equation 2, Suter & Wildman 1999; column 4, from regression in Fig. 8; column 6, from Suter & Wildman 1999.

Spider mass g	Estimated leg length mm	Force required for static support mN	Force required for jumping mN	Total resistive force required mN	Force available from dimple mN
0.050	11.5	0.061	0.265	0.326	0.875
0.150	17.8	0.184	0.717	0.900	1.271
0.250	20.8	0.306	1.169	1.475	1.437
0.350	22.7	0.429	1.620	2.049	1.555
0.450	24.1	0.551	2.072	2.623	1.662
0.550	25.3	0.674	2.524	3.198	1.733
0.650	26.3	0.796	2.976	3.772	1.792
0.750	27.1	0.919	3.428	4.346	1.816

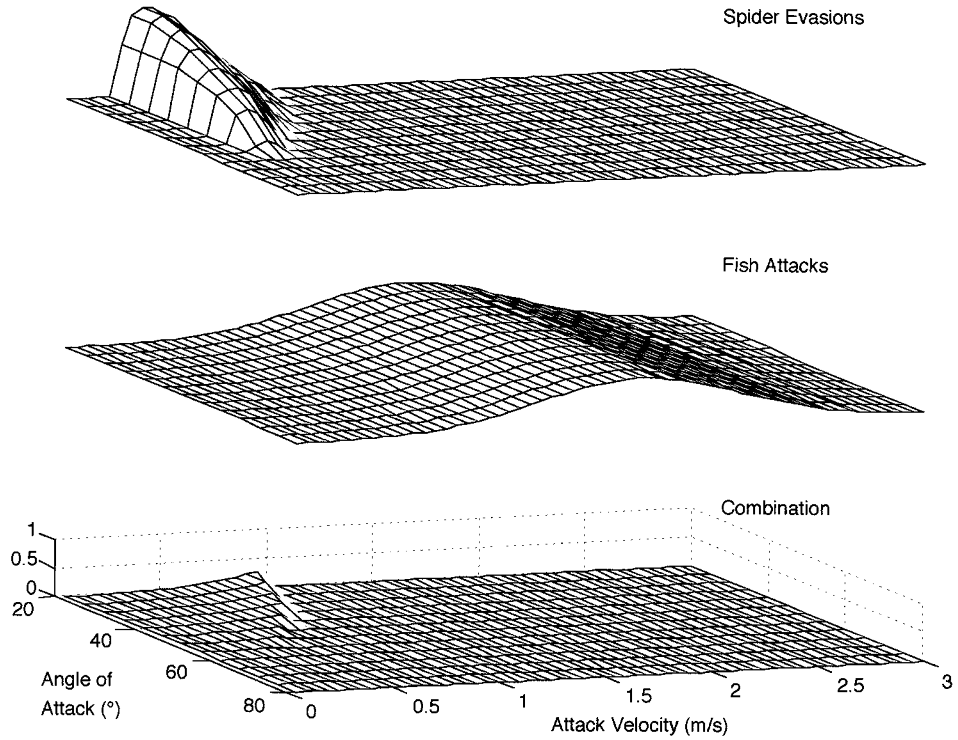

Figure 10.—Evasion success (top) and the actual attack dynamics of trout (middle), when combined, reveal a very small area of overlap on the velocity *vs.* angle-of-attack plane (bottom). This example depicts results for a 0.25 g spider with a 2 cm detection distance.

DISCUSSION

We began this study under the assumption that vertical jumps from the water surface by *D. triton* function to decrease the probability of capture by fish attacking from below. Implicit in our assumption was the presumed role that natural selection had played in shaping both jump latency and jump height (and duration), with the result that vertical jumping from the water surface, as currently practiced by fishing spiders, would be an effective evasive behavior. We have demonstrated, on the contrary, that jumping could save spiders in only a very small fraction of attacks by fish (Fig. 10). At the root of this ineffectual capacity are the size-independent maximum height of jumps (about 3.67 cm) and their correspondingly brief duration (about 0.17 sec), and at the root of the limited jump height is the quality of the interaction between the spiders' legs and the water.

Fluid drag ultimately provides the resistance against which the spider pushes (Fig. 8; Suter & Wildman 1999). It follows that anatomical modifications to a spider's legs such as lateral expansions (via hairs or cuticular shape changes), which would expand the area of the surface perpendicular to the direction of the legs' motion during jumping, would increase drag and allow a more rapid upward acceleration of the spider. The more rapid acceleration would cause both jump height and jump duration to rise and would render the spider less vulnerable to predation by fish. The absence of such expansions suggests (a) that predation by fish constitutes a relatively mild selective force on these fishing spiders, (b) that contrary selective pressures (e.g., those fostering efficient rowing or prey capture) prevail, or (c) that lateral expansion is phylogenetically constrained. We have no data that allow us to discriminate among these three possibilities and note that any or all of them could operate simultaneously.

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