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Trichobothrial mediation of an aquatic escape response: Directional jumps by the fishing spider, *Dolomedes triton,* foil frog attacks

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Abstract

Fishing spiders (Pisauridae) frequent the surfaces of ponds and streams and thereby expose themselves to predation by a variety of aquatic and semi-aquatic vertebrates. To assess the possibility that the impressive jumps of fishing spiders from the water surface function in evading attacks by frogs, attacks by bullfrogs (*Rana catesbiana*) and green frogs (*R. clamitans*) on *Dolomedes triton* were studied. Both the attack dynamics of the frogs and the evasive behaviors of the spiders were recorded at 250 frames per second. A freeze-dried bullfrog, propelled toward spiders with acceleration, posture, and position that approximated the natural attack posture and dynamics, was used to assess the spiders' behavior. Qualitatively, the spiders responded to these mock-attacks just as they had to attacks by live frogs: jumping (N=29 jumps, 56.9% of instances), rearing the legs nearest the attacking frog (N=15, 29.4%), or showing no visible response (N=7, 13.7%). Spiders that jumped always did so away (in the vertical plane) from the attack (mean =137° vs. vertical at 90° or horizontally toward the frog at 0°). The involvement of the trichobothria (leg hairs sensitive to air movements), and the eyes as sensory mediators of the evasion response was assessed. Spiders with deactivated trichobothria were significantly impaired relative to intact and sham-deactivated spiders, and relative to spiders in total darkness. Thus, functional trichobothria, unlike the eyes, are both necessary and sufficient mediators of the evasion response. Measurements of air flow during frog attacks suggest that an exponential rise in flow velocity is the airborne signature of an attack.

Keywords: Rana catesbiana, *Rana clamitans*, predatory behavior, sensory ecology

Abbreviation:

a	acceleration (m s^{-2})
fps	frames per second
HS	high-speed video
v	velocity (m s^{-1})

Introduction

Fishing spiders (Pisauridae) spend much of their lives at the edges of ponds and streams, venturing out onto the water surface to capture insects, small fish, and tadpoles, and to escape from terrestrial predators such as wading birds. They move across the water surface with ease (Gorb and Barth, 1994; McAlister, 1959; Shultz, 1987; Suter *et al.*, 1997), either rowing at velocities < 0.2 m s^{-1} or galloping at velocities > 0.3 m s^{-1} (Suter and Wildman, 1999). They can even sail, with legs or body raised well above the surface, when conditions permit (Deshefy, 1981; Suter, 1999). Males find females, in part, by following the females' pheromone-impregnated draglines on the water surface (Roland and Rovner, 1983), and both sexes find prey by detecting the surface waves created as insects struggle to escape the adhesive energy of the surface tension (Bleckmann, 1985; 1994; Bleckmann *et al.* 1994). The spiders' adept exploitation of this semi-aquatic habitat not only gives them access to an expanded array of potential prey but also exposes them to predators, including fish and frogs, that they would not otherwise encounter.

Attacks by fish and frogs may well have exerted selective pressure on these spiders sufficient to shape their behavior and reduce their vulnerability. Previous work has shown that the impressive jumps of fishing spiders from the water surface are unlikely to function well in evading attacks by fish from below (Suter and Gruenwald, 2000). The relative futility of the jumps in response to attacks by fish is due in part to the high velocity of fish attacks and in part to the fact that, during an attack, both predator and prey are moving in approximately the same direction, upwards.

These same jumps, however, especially if responsive both to the timing and to the direction of attacks, might well function in the avoidance of predation by frogs. This possibility was evaluated

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first by studying attacks by bullfrogs (*Rana catesbiana*) and green frogs (*R. clamitans*) on *Dolomedes triton* (Araneae: Pisauridae). The responses of initially motionless spiders to simulated attacks by a freeze-dried bullfrog was then evaluated and the roles of the eyes and the air movement-sensitive hairs (trichobothria) on their legs in mediating the evasive responses was assessed. Finally, the air movements that accompany frog attacks were recorded and the airborne signature of a frog attack, to which the spiders may be responding, was identified.

Materials and Methods

Subjects

The fishing spiders (*D. triton*) used in this study were collected at the edges of ponds in northwestern Mississippi, USA. Both adult and sub-adult spiders were used, and both males and females, all of which had been in captivity for at least several weeks. The spiders were maintained in 245-ml polystyrene cups which were filled to a depth of approximately 1.5 cm with distilled water and covered by the top half of a disposable plastic petri dish.The spiders were fed with commercially available crickets (*Acheta domestica*) and mealworms (*Tenebrio molitor*), occasionally augmenting the diet with freshly captured moths, crickets, leaf hoppers, and flies.

Bullfrogs (*Rana catesbeiana*) and green frogs (*R. clamitans*) were captured with a fishing net from the edges of ponds on the campus of Vassar College, Poughkeepsie, New York, USA, but only those with snout-to-vent lengths exceeding 10 cm were retained. All frogs were used within 24 h of capture, were returned to the ponds from which they had been taken, and were handled in accordance with Protocol #01-10B, as approved by the Vassar College Institutional Animal Care and Use Committee.

Attacks by frogs on spiders

The test arena for observing attacks by frogs on spiders was a 202-liter aquarium (90 X 45 X 50 cm) with approximately 5 cm of pond water covering a layer of gravel. This water depth allowed a frog to rest on the gravel with its head just above the water surface, and permitted it to move about by walking and hopping rather than by swimming. The arena was illuminated by a 250-W NorthStar® halogen lamp (Photographic Analysis Co., www.visiblesolutions.com/pac.html) located approximately 1.5 m above the water surface. A video camera (Panasonic GP-KR222, www.panasonic.com) was used, mounted 1.5 m above the center of the arena, feeding images to an S-VHS recorder (JVC HR-S5400U) to provide a continuous record (at 30 fps) of the motions of the frog and its quarry. From this view the direction, in the horizontal plane, of the attacks of the frog could be measured. The camera of a high-speed (HS) video system (MotionScope S series, Redlake Imaging Corporation, www.redlake.com), operating at 250 frames per second (fps) was mounted 105 cm from the front of the arena with the lens at the same level as the water surface. When in record mode, this HS video system stores approximately 1600 images in a digital buffer, continuously renewing the buffer by discarding the oldest frame as each new frame is captured. Recording was halted in the HS system at the end of each attack and thereby had access to the 1600 frames that had been stored in memory prior to triggering the halt. The continuous monitoring from the overhead camera was interrupted to record, onto the same tape, the images of an attack from the HS video system.

The four vertical sides of the arena were surrounded with an opaque screen the front of which was 100 cm from the front surface of the arena. The only opening in the screen was an oblong rectangle (30 long X 8 cm high) to provide a view port for the HS camera.

During an individual test, the frog was first placed in the fully lit arena and allowed to acclimate to the unfamiliar

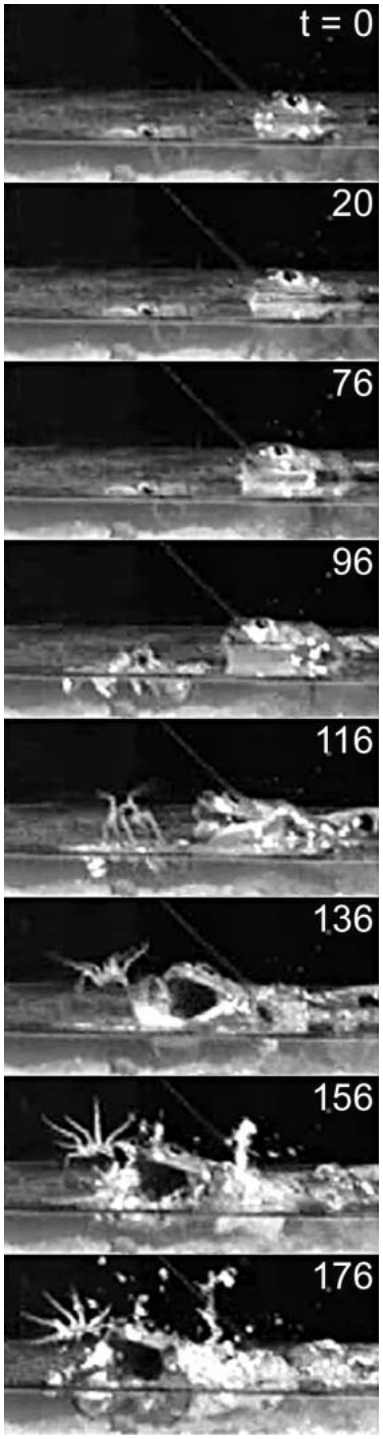

Figure 1. High-speed videographic frames depicting an attack by a bullfrog on a fishing spider. Both animals were initially at rest (top). Elapsed time (ms) is shown for each frame. In this trial the spider escaped uninjured.

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surroundings for at least 15 min. The test spider, temporarily held in a high-density polyethylene cup, was dropped into the arena from the top so that it landed on the water at least 50 cm from the frog. From that point on taping was done continuously, both at 30 fps from above and at 250 fps from the front (Fig. 1), until the completion of an attack. The full record of an attack consisted of the two video segments and hand-written notes on the outcome (spider consumed, unharmed, missing two legs, etc.).

The view from above was used to plot the true horizontal trajectory of an attack. That true trajectory and the known location of the HS camera made possible the trigonometric conversion of the relative velocities and accelerations (measured during frame-by-frame analysis in NIH Image) detectable on the HS video images to absolute velocities and accelerations.

The subject pool consisted of 7 frogs and 24 spiders. Because the frogs' appetites appeared not to diminish with each successful capture, each frog was used multiple times, with at least 5 min between each test. In two tests the same frog/spider combination was used a second time. Because the functions of these tests were (a) to measure attack dynamics and (b) to assess under somewhat controlled conditions the success of evasion attempts, the data from the two repeated uses of the same frog/spider combinations were not eliminated.

Simulated attacks on live spiders

The model predator (henceforth, the "model") for simulated attacks on live spiders was the freeze-dried carcass of an adult male bullfrog (Ward's Natural Science), modified as follows. The hind legs were removed 1 cm distal to the pelvis-femur joint; the carcass, now 15.5 cm long, was painted with a white, rubberized coating (Plasti Dip®, PDI, Inc., www.plastidip.com) and spot-coated with clear silicone sealant to render it waterproof; and a bolt passing through the carcass from ventral to dorsal surfaces 2 cm anterior to the anus secured the model to a 7-cm length of CPVC pipe (OD = 16 mm).

The model was attached to the lowest point of the long arm (78 cm) of an Γ -shaped lever system (Fig. 2) in which the fulcrum was at the intersection of the two arms. Hanging from the end of the short arm was a 0.5-kg mass which, when accelerated by gravity, propelled the model in a nearly horizontal trajectory. The length of the short arm was adjusted to achieve a model acceleration that approximated the mean acceleration observed during attacks of live frogs on spiders.

Prior to a test, the short arm of the lever was held horizontal by a solenoid-actuated catch. A light beam, interrupted by the long arm of the lever when the system was in its cocked position, activated a photodiode once the lever was in motion. The photodiode served to trigger the HS video system, this time set to collect 1600 images *after* sensing the trigger, when the test was being run under lighted conditions, and to start a delay circuit (LPA Time Machine®, LPA Design, Inc.) set to trigger a photographic strobe light when the test was being run in darkness. The delay circuit was adjusted to match the time between the start of an actual attack and the moment when, in an average evasion jump, the spider was fully clear of the water surface. Under these conditions, the model's attack took place in complete darkness until the scene was illuminated by a single flash (< 1 ms duration) 0.12 s after the attack began.

Figure 2. Side view of the lever system used to propel the model frog toward a spider at rest on the water surface (bottom left). At the start of a trial, the horizontal arm is released by a solenoid (top right), the suspended mass accelerates downward, and the model frog accelerates to the left.

At the start of a test, the model was at one end and facing toward the center of a 39-liter aquarium (50 X 26 X 30 cm), partially submerged in water that was about 5 cm deep. The test spider was then placed on the water surface, and allowed to calm down for 3-5 min. It was then gently moved (using a slender glass rod or gentle puffs of breath) into the start position. The start position was directly in front of the model (Fig. 3), at a distance that approximated the average distance from frog to spider in the live frog attacks, with the spider approximately facing the model. Tests were discarded when the spider moved before the simulated attack was triggered.

The 21 test spiders were randomly divided into four treatment groups designated as Intact (N= 6), Smear (N= 4), Cool (N= 5), and Dark (N= 6). Intact and Dark spiders were not manipulated prior to testing. Spiders were anesthetized in the Smear and Cool groups by placing them on ice at 0° C for 15 min. A thin film of silicone vacuum grease (Beckman Instrumets, Inc., www.beckman.com) was then smeared on the upper surface of the femur tibia and tarsus of each leg of the spiders in the Smear group. Grease was not placed on any joint. Because the grease was confined to the upper surface of the legs and was kept away from the joints, interference with the spiders' locomotion should be minimal. However, because smearing the joints was avoided, some trichobothria (Fig. 4) both exposed and functional. Spiders in the Cool group were anesthetized but not manipulated in any other way and served as controls for the effects of thermal anesthesia in the Smear group. Each spider was tested 3-8 times, with a rest period of 4-6 min between each test. A test was scored as 0 if the spider made no visible response,1 if the spider reared the legs nearest to the model, and 2 if the spider leaped from the water surface in response to the simulated attack (Fig. 5). The mean of the scores for each spider was taken to be the spider's single score for the

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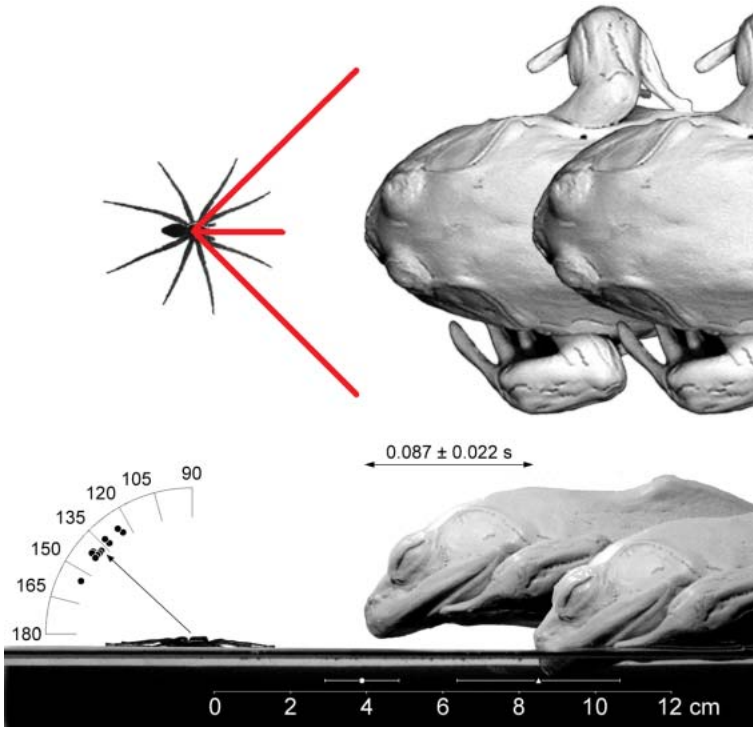

Figure 3. Top and side views of a fishing spider (left) and model frog (far right), both at rest at the start of a trial and separated (mean ± SE) as shown on the cm scale. Only trials in which the spider was facing the frog model (± 45°, red lines) were used in this study. The distance scale indicates the position of the model from the spiders at the start of the trials (filled triangle; mean ± SE) and its position at the moment when each spider first made a visible response to an attack (filled circle). If the spider responded it did so, on average, about 87 ms after the initiation of the attack (horizontal double-headed arrow; mean ± SE). Leaps by the spiders, when they occurred, were inclined in the vertical plane (filled circles on the polar plot) at an angle of about 137° away from the model. Measurements of air flows during mock attacks (in the absence of spiders) were made with the sensor wire of an anemometer located at the vertex of the red lines, 2 mm above the water surface.

purposes of statistical analysis.

Measurement of air movement

A hot-wire anemometer (Thermonetics Corporation [www.electriciti.com/~thermo/tc.html], model HWA-103; frequency response > 500 Hz) was used to measure air movement above the water surface in the laboratory during model attacks. Data were collected at 100 Hz using a LabPro digitizer driven by LoggerPro software (Vernier Software and Technology, www.vernier.com) on a Macintosh G3 platform, and then applied a high-pass FFT filter (30 Hz cutoff) in Origin (Microcal Software, Inc., www.microcal.com) on a Windows NT platform (Dell 620 PC workstation) to eliminate low frequency fluctuations caused by ambient conditions in the laboratory.

The wire sensor (length = 3 mm) of the anemometer was placed on the axis of movement of the model (i.e., directly in front of the model), parallel to the water surface at a height of 2 mm, and at an initial distance from the model that approximated the initial distance between the model and the spiders (Fig. 3). Air velocity data were collected under these conditions from five seconds before a model attack until the attack was complete.

Results

Attacks by frogs on spiders

Attacks by 30 bullfrogs and green frogs on *D. triton* were recorded under laboratory conditions. Most of the attacks (21, 70%) were successful from the frogs' perspective. During five of the attacks (16.7%), the spiders leaped from the water surface as if to evade the attacks (Fig. 1), and in four of those attacks (13.3% of the total, 80% of the evasion attempts), the spiders escaped unscathed (Video 1). The four attacks not listed above included one in which the frog entirely missed a galloping spider and three in which the spiders remained unharmed but I could not discern from the tapes whether the spiders had made any attempts at evasion.

The dynamics of the seven recorded attacks that met the criteria for clarity were analyzed The HS camera was not panning during the attack and the direction of attack was no closer than 30° to an imaginary line joining the frog and the camera lens. At the start of an attack, the frog and spider were separated by 9.90 ± 2.33 cm (mean ± SE). Velocity increased linearly with time during each attack ($r^2 = 0.96 \pm 0.01$ for the seven linear fits to the data), allowing the calculation of the frogs' accelerations as 15.61 ± 1.97 ms^{-2}, the equivalent of 1.59 G. Maximum attack velocities varied between 0.76 and 1.72 ms^{-1} (1.29 ± 0.19 ms^{-1}).

Simulated attacks on live spiders

Model "attacks" on spiders were triggered when the spider and model were separated by 8.64 ± 1.93 cm (N = 20 runs in the Intact group). If the spider reared or leaped, it made its first detectable motion 0.087 ± 0.022 s (N = 16) after the start of the model's lunge while the two were still separated by 3.87 ± 0.97 cm (N = 16). If the spider leaped, its leap carried it in a direction away from the model in the vertical plane (137.1° ± 7.7°, relative to 0° toward the model and 90° perpendicular to the water surface; significantly non-random, z = 11.783, P < 0.001, N = 12) (Fig. 3).

In 77 model attacks, the spiders leaped 34 times (44%;

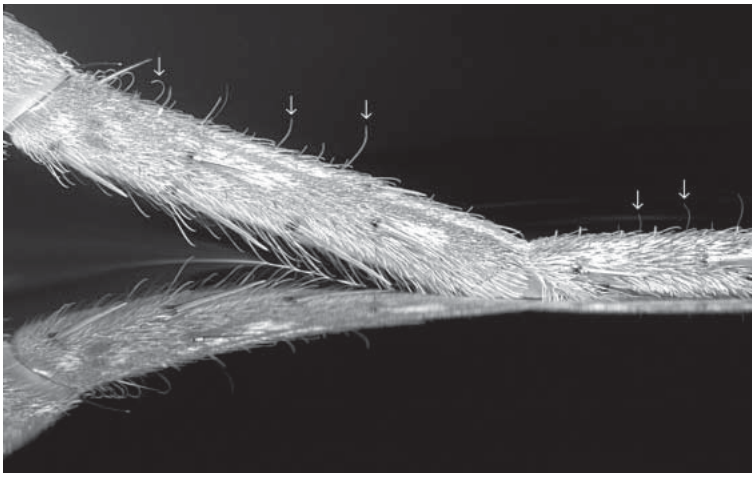

Figure 4. Side view of patella (left),tibia, and metatarsus (right) of leg (II) of the fishing spider, *D. triton*, on the water surface. Trichobothria, the long upright hairs (some indicated by arrows) along the dorsal surface of the tibia and metatarsus, some with curved distal ends, inform the spider about air movements.

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Video 2), reared 22 times (29%), and remained motionless 21 times (27%). These behaviors were not randomly distributed among treatments. Using the spider score (see methods), spiders in the Intact, Cool (thermal anesthesia but no silicone smear), and Dark groups were not significantly different from each other but were significantly more likely to leap or rear than were spiders in the Smear group (Fig. 6; ANOVA, $F = 6.51$, $P = 0.005$).

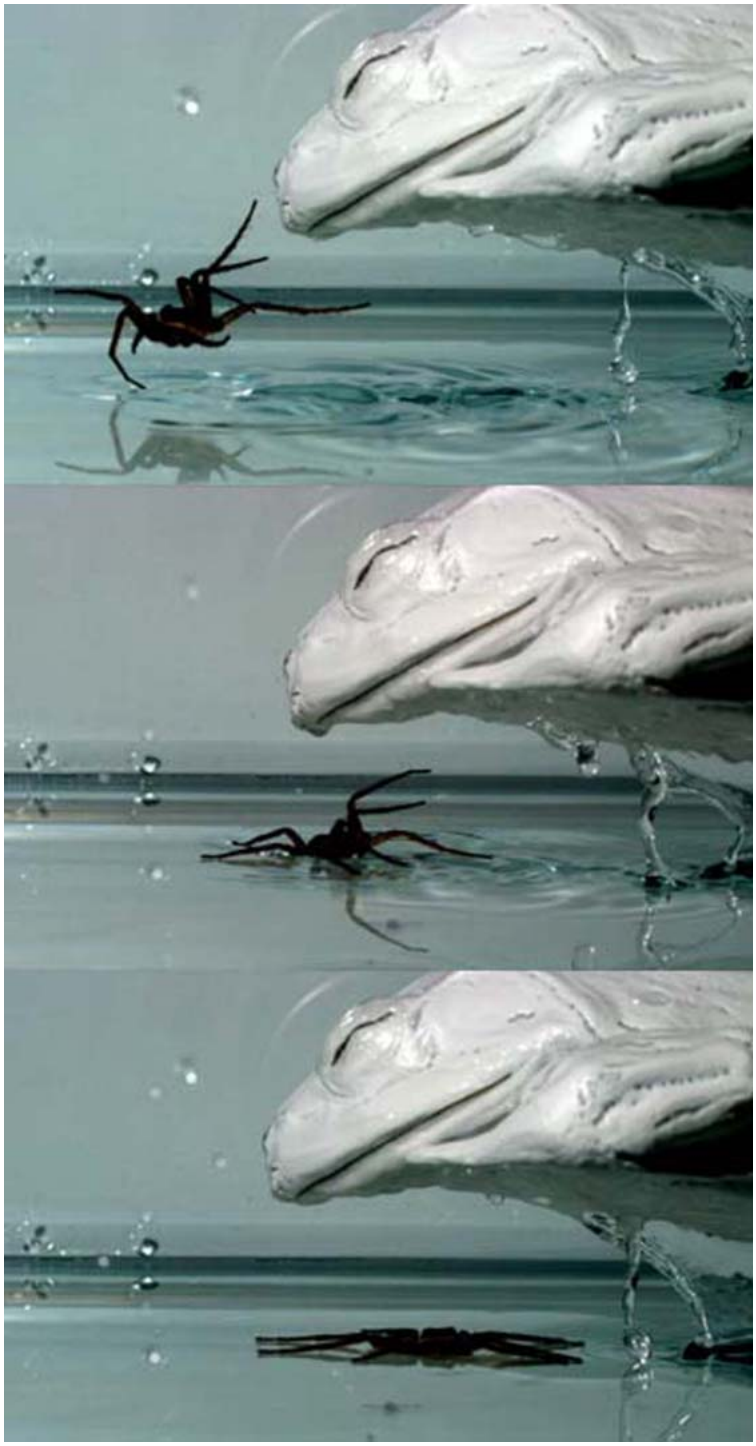

Figure 5. Three independent responses to the lunge of the frog model: the spiders leaped from the water surface (top) by pushing their legs downward, reared the legs nearest to the model (middle), or remained motionless (bottom). These responses were given scores of 2, 1, and 0, respectively. Each image was made 0.12 s after the start of the simulated attack.

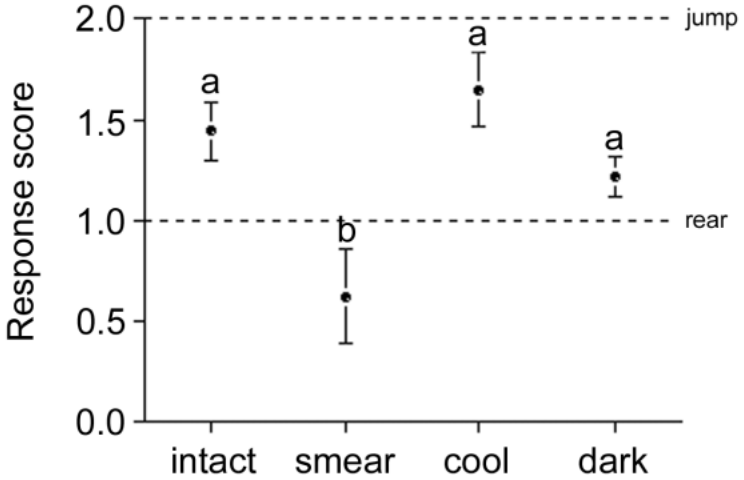

Figure 6. Responses of spiders to lunges of the model frog. Intact spiders that were in the light, that had been cooled prior to testing, and that were in the dark, usually either reared or leaped, resulting in scores between 2 (jump) and 1 (rear). Spiders with most of their trichobothria disabled (smeared) usually remained motionless or reared. Differences among these four treatments were highly significant (ANOVA, $F = 6.51$, $P = 0.005$). Post hoc tests indicated that the Smear scores were significantly lower than those of each of the other groups (Fisher's PLSD, $P < 0.05$), and that there were no significant differences between the other groups.

Measurements of air movement

Anemometer measurements were collected during 16 model attacks in which the anemometer sensor, at 2 mm above the water surface, took the place of the spider's trichobothria. A model attack was invariably characterized by a rapid rise in air velocity (v, m s^{-1}) (Fig. 7) as a function of time (t, s). The mean of these velocities closely ($r^2 = 0.995$) followed the line described by

$$\boldsymbol{v = 416t^3 - 30t^2 + 0.89t + 0.008} \quad (1)$$

and permitted calculation of the acceleration (a, m s^{-2}) as

$$\boldsymbol{a = 1248t^2 - 60t + 0.89}. \quad (2)$$

Discussion

Under laboratory conditions, fishing spiders sometimes leaped from the water surface when attacked by bullfrogs and green frogs. When they did not leap, they were nearly always consumed, but when they did leap, they usually escaped unscathed. Both the effectiveness of the leaps in evading attacks (Fig. 1) and their directionality (Fig. 3) suggest that leaping from the water surface is an adaptation that functions in predator evasion. Having determined that these leaps are far more effective when applied to frog attacks than they could be in response to attacks from below by fish (Suter and Gruenwald, 2000), the question became what sensory systems detect the signals that trigger an evasive leap at the appropriate moment.

Spiders have vision, usually via 6 or 8 simple eyes (Barth *et al.*, 1993; Blest and Day 1978; DeVoe *et al.* 1969; Land, 1985), olfaction via chemosensory hairs (Foelix, 1970; Pollard *et al.*, 1987), a vibration/tactile sense on solid and liquid substrates via slit sensilla (Barth, 1978; Bleckmann 1985; Bleckmann *et al.*, 1994; McIndoo, 1911; Pringle, 1955), airborne vibration and rheoreception via trichobothria (Barth, 2002; 1985 and references therein), and

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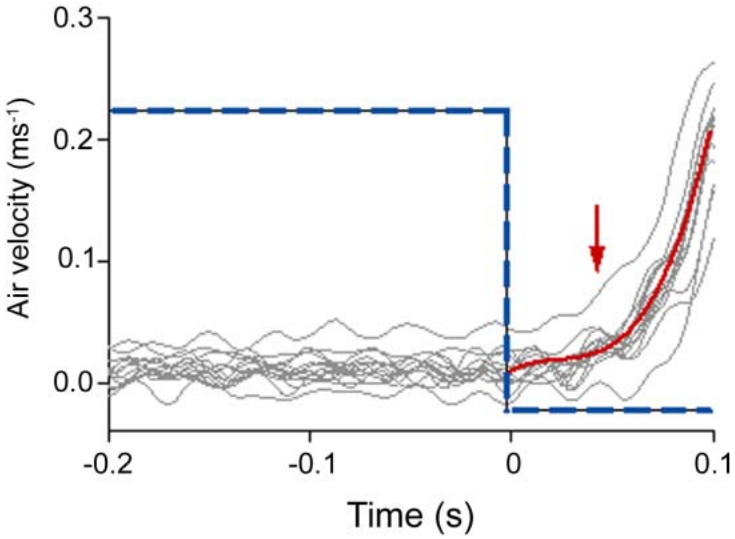

Figure 7. Air movements detected by a hotwire anemometer, with the sensor 2 mm above the water surface, during lunges of the model frog. The vertical portion of the dashed line indicates the moment when the model began its acceleration. Gray lines show individual trials (N = 16). The solid red line shows the average of the air velocities during the first 0.1 s of a model attack. A 3rd order polynomial fit to this line constituted the air-borne signature of an attack (Eq. 1). The red arrow indicates the first time at which both the air velocity and its acceleration exceeded the values found to trigger escape behavior in similarly attacked cockroaches (Camhi *et al.*, 1978).

thermoreception (Ehn and Tichy, 1996). Among these senses, all but olfaction and thermoreception could conceivably be involved in the fishing spider's detection of a frog attack.

Because the spiders in the experiments reported here responded as well in complete darkness as they did in the light (Fig. 6), the conclusion that vision is not involved in mediating the evasive leaping behavior is justified. Moreover, a central role for the trichobothria was confirmed in the same experiment by the sharp reduction in response when many of those sensory hairs were rendered inoperative (Fig. 6). The same data that demonstrate the central role of the trichobothria, also eliminate the sensing of waves on the water surface by the lyriform organs, proprioceptive slit sensilla located at each leg joint, as being important in triggering the evasive behavior. If those organs were important for this behavior, then the spiders with grease-smeared legs (with the joints unimpaired) would have responded to model attacks with the same sensitivity as demonstrated by the intact animals. A second line of reasoning also eliminates a functional role for surface-borne waves. The hull speed of the15.5-cm long model frog, that is, the speed of the bow wave it produces as it moves through the water, is 0.49 m s^{-1} (Denny 1993). This is close to the average velocity of the model frog (0.55 m s^{-1}) during the initial 0.087 s of its lunge. Thus, at the moment that the spider began either rearing or jumping, the bow wave was still about 3.9 cm from the spider (Fig. 3) and could not have alerted the spider to the simulated attack. Clearly, air movements associated with the model frog's lunge and detected by the spider's trichobothria mediate the spider's evasive response.

The directionality of the fishing spiders' leaps (Fig. 3) indicates that the spiders glean spatial information during integration of the trichobothrial stimuli. In light of the known capabilities of the trichobothria and their underlying sensory circuits (Barth and Höller, 1999; Friedel and Barth, 1997; Reissland and Görner; 1985), this directional sensitivity is not surprising. For example, in *Cupiennius salei*, a wandering spider in the family Ctenidae (related to the Pisauridae, of which *Dolomedes triton* is a member, all within the Lycosoidea [Silva Davila, 2002]), certain interneurons respond preferentially to the sequential stimulation of trichobothria on adjacent legs and respond differentially to the order of stimulation (Friedel and Barth, 1997). Assuming that the frog's airborne attack signature propagates along a wave front at least as broad as the attacking frog, the fishing spider would receive aerodynamic input on all eight legs thereby providing a plethora of directional data with which to calculate the appropriate evasion direction.

The attacks of the model frog were preceded (from the spider's perspective) by moving air that was rapidly accelerating (Fig. 7; Eq. 2). Camhi *et al.* (1978) determined that a two conditions of air motion ($v > 12$ mm s^{-1}; $a > 600$ mm s^{-2}) were required to elicit the escape response of a cockroach (*Periplaneta americana*) by the attack of a toad. These same conditions were satisfied 43 ms after the start of a frog attack (Fig. 7), still about 44 ms before the first detectable response from the spider (Fig. 3). Thus it appears that the sensory hairs on the cerci of the cockroach and the trichobothria on the legs of the fishing spider are functionally similar and that the escape responses are triggered by quantitatively similar stimuli. Another rapid escape response, the tail-flip of crayfish (e.g., *Procambarus clarkii*), is also elicited by the displacement of directionally sensitive cuticular hairs (Edwards et al., 1999 and references therein) and occurs with similar timing. The spider's evasive leap from the water surface, then, can be seen as one of a class of strong, rapid, reflexive responses to abrupt fluid (air or water) disturbances.

The findings presented here indicate (1) that fishing spiders on the water surface respond with evasive leaps when attacked horizontally by frogs, (2) that the trichobothria mediate this response by sensing the air movements that accompany an attack, and (3) that the airborne signature of an attack is probably a very rapid acceleration of air flow. A number of questions remain. For example, to what extent do the movements of the spider itself cause trichobothrial stimulation that could mask detection of a frog's attack? If such interference does occur, then the risks of motion would be compounded; the motion itself would increase the probability of attacks by frogs because of anurans' retinal motion detectors (Ewert, 1987) and the spider would be less capable of detecting the attacks. Cockroaches appears to have solved this problem (Plummer & Camhi, 1981) and it will be interesting to determine whether fishing spiders have done so as well. A more general and less tractable question is this: In the evolution of the trichobothrial sensory system, how have predator detection (this study), prey detection (Barth and Höller, 1999), and other functions interacted to produce the system with its current properties?

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