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Spider's attack versus cricket's escape: velocity modes determine success

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The behavioural and physical mechanisms involved in the tactics used by predators to catch their prey have been explored for a wide variety of vertebrate taxa but most studies have considered the viewpoints of predator and prey independently. We tackled this issue using an ecologically relevant predator–prey model: wolf spiders (*Pardosa* spp.) and wood crickets, *Nemobius sylvestris*. Crickets are particularly challenging prey to catch because their air-sensing systems enable them to detect small air movements caused by approaching predators. Using a high-speed video camera, we found that freely behaving spiders adopted either a fast or a slow velocity tactic to approach crickets. We then developed a device using a piston to simulate, as faithfully as possible, the spider's attack. The air flow generated by the piston was quantified by particle image velocimetry and then used to test the escape success of crickets at different attack velocities. Cricket escape success was lower for low and high piston velocities, matching the two tactics adopted by the spiders. Based on our results, we propose that the escape probability of prey after a given predator signal can be explained by the distance between the prey and the predator, the velocity of the predator and the strength of the signal. Both methodological and conceptual approaches presented in this study could provide useful methods to understand the biological and physical basis of predatory tactics in other animals.

The behavioural and physical mechanisms involved in the tactics used by predators to catch their prey have been investigated for a wide variety of vertebrate taxa including fish (Webb & Skadsen 1980; Domenici & Blake 1997), amphibians (Gans & Gorniak 1982; Deban 1997), insectivores (Catania & Remple 2005) and bats (Jones & Rydell 1994; Kalko 1995). These studies have attempted to answer a number of questions. What is the nature of stimuli generated by the predator during different types of attack? What are the conditions that induce prey escape? What is the escape probability of the prey as a function of predator tactic? From the perspective of prey, the biomechanics and/or the neuroethology of escape have also been thoroughly studied in various models including insects (Gnatzy 1996), crustaceans (Herberholz et al. 2004), fish (Domenici & Blake 1997) and passerine birds (Kullberg et al. 1998; Lind et al. 2003). Surprisingly, most studies on mechanisms involved in predator–prey interactions have considered the viewpoint of predator and prey independently.

Few integrated approaches, with the notable exceptions of the bat–moth model (Fullard 1987), the spider–fly model (Barth 2002) and the frog–spider model (Suter 2003), have included a view of both partners. The lack of studies considering both predator and prey is likely to hamper our understanding of evolutionary forces that shape tactics used by predators and prey in nature (Abrams 2000; Lima 2002).

Predator tactics must be finely tuned when predators face prey possessing high-performance detection systems. Crickets, for example, are one of the most challenging prey to catch. Their air movement sensory system, as for other Orthopteroïds (e.g. cockroaches), is a classic example in neuroethology textbooks (reviewed in Camhi 1984; Gnatzy 1996). These insects bear on their cerci hundreds of mechanoreceptive hairs that enable them to sense the faintest air movements generated by approaching predators (Gnatzy 1996). The extreme sensitivity of crickets' wind-detecting system allows them to use air flow patterns for detecting predators, even at relatively large distances (up to 30 times their body length, Gnatzy & Kämper 1990; Dangles et al. 2005). The highly sensitive warning system therefore allows crickets to escape successfully, conferring on them an obvious selective advantage (Endler 1986).

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To our knowledge, only one example of a predator–cricket interaction has been studied in the field: the hunting wasp, *Liris niger*, and the house cricket, *Acheta domesticus* (reviewed in Gnatzy 1996). Gnatzy and other researchers have stressed the importance of air flow signals generated by the wasp that initiate a response by the cricket (see Gnatzy 1996 and references therein). However, they did not tackle the question of what kind of predatory behaviour would be best to overcome the defences of crickets.

Although house crickets are a natural prey of *Liris* wasps, we do not know whether these predators are a major threat to most crickets and how much they impact on cricket fitness. These missing pieces in a predator–prey model are due to the difficulty of observing and quantifying predator–prey processes in the field. Wood crickets, *Nemobius sylvestris*, and wolf spiders (Lycosidae, *Pardosa* sp.) are another good candidate system for the study of predator–prey interactions in the field, in an ecologically relevant context. Wood crickets are widespread and common on deciduous forest floors, reaching high densities in both space and time (Gabbutt 1959). Owing to their small size and foraging habits, they are exposed to a wide range of predators hunting on the ground including wolf spiders. These spiders hunt either by waiting motionless, ready to snap, or by a fast active pursuit (Ford 1977). Extensive observations of predation events in the field showed that juvenile wood crickets are important prey items in the diet of wolf spiders (Gabbutt 1959; Edgar 1969; O. Dangles, personal observation) and that wolf spiders are an important mortality factor (Dangles et al. 2006).

In the present study, we conducted three experiments to study the underlying mechanism of the interplay between wood crickets and wolf spiders. We first aimed at quantifying the behavioural tactics used by spiders to attack crickets. Second, we developed a piston to simulate, as faithfully as possible, the stimuli generated by spiders. Natural predator–prey interactions with prey possessing excellent detection systems are bound to end with many more escapes than captures. Therefore, using a proper bioassay becomes a priority for increasing the number of observations (e.g. Friedel & Barth 1997; Suter 2003). The piston is a noninvasive device that allows us to study the cricket's response to a predator's signal without harm and with limited stress for the animals. Third, we used this bioassay to quantify the escape success of crickets to artificial signals approaching at different speeds. This enabled us to interpret the results obtained in the first nonmanipulative experiment conducted with living spiders.

EXPERIMENT 1: CRICKET–SPIDER INTERACTIONS

Methods

We collected immature wolf spiders and sixth-instar wood crickets from an oak forest in the vicinity of Tours, France (47°17′06″N, 00°47′13″E). The juvenile spiders were probably a mixture of the sibling species *P. amentata* Clerck and *P. lugubris* Walckenaer, based upon identification of mature males from the collecting sites. We used only immatures because they naturally spend much of their time foraging and not seeking partners. In the laboratory, spiders were isolated individually without food for 2 days before the behavioural tests. Food withdrawal is a common procedure meant to homogenize levels of hunger among individuals (Persons et al. 2001). Food deprivation periods of up to 10 days have no apparent detrimental effect on spiders (Barnes et al. 2002). Crickets were kept in a separate cage with water and cat food provided ad libitum.

The interactions between spiders and crickets were observed in a plastic arena (28×28 cm and 7.5 cm high). For each trial, a single cricket and a single spider were introduced into the arena. We allowed each spider to make only one strike after presentation of one cricket so that stress to the cricket was minimized. Crickets could escape either by running or jumping away from the spider, eventually out of the box as was occasionally the case. Cricket–spider interactions were filmed at 55 frames/s under 300 µW/cm² illumination using a video camera (Euromex, Arnhem, The Netherlands). The temperature of the floor of the arena was 25 °C and the relative humidity was 60%. Because cricket cerci are predominantly used to detect predator attack from the rear (Gnatzy 1996), we kept only those videos showing spiders attacking crickets at ±45° from the rear for subsequent analyses. According to Campan et al. (1976), who studied the spatial discrimination of shape in *N. sylvestris*, this precaution enabled us to exclude the possibility that crickets could see the spiders. Trials were terminated after 10 min if no attack had occurred. We measured (1) the distance at which the spider launched its attack (measured between the spider's head and the rear end of the cricket's cerci), (2) the distance at which the spider's attack triggered the cricket's escape, (3) the kinematics of the spider's run, especially the duration of the acceleration phase and (4) the mean spider's attack velocity once constant.

To characterize the distribution of spider attack velocities, we determined the set of overlapping component distributions that gave the best fit to our data by using a combination of a Newton-type method and expectation maximization (EM) algorithms. Briefly, EM alternates between performing an expectation (E) step, which computes the expected value of the latent variables, and a maximization (M) step, which computes the maximum likelihood estimates of the parameters given the data and setting the latent variables to their expectation (Meng & van Dyk 1997; Neal & Hinton 1999). These analyses allow the classification of the observed data into different subpopulations (Pawitan 2001) and are therefore particularly suited to test the significance of different predatory tactics by the spider. Proportion (P_i), mean (μ) and variance (σ) for each component distributions were calculated with the 'mixture distribution' package of R software (www.r-project.org).

Results

After they were placed in the test arena, spiders usually remained motionless while crickets explored the chamber.

When the cricket entered the visual field of a spider, the spider turned towards the cricket in preparation for an attack. In contrast, the cricket displayed no change in behaviour and continued its exploration. Only if the cricket came within 2–7 cm did the spider launch its attack, and it did so at a median distance of 4.5 cm (Fig. 1a). On average, crickets escaped after the spider came to within 1.4 cm (Fig. 1b). Typical escape behaviour consisted of an initial 90° pivot of the cricket before escaping. The kinematics of the spider's run was composed of a short initial acceleration over 1 cm followed by a phase with relatively constant velocity up to the moment when it reached the prey (Fig. 1c). In the rest of the text, the term 'velocity' refers to the phase of constant velocity.

Attack velocities by spiders ranged from 2 to 41 cm/s (Fig. 2). The fitted mixed distribution of the 49 observed attacks revealed two main tactics: 76.4% of spiders' attacks preferentially occurred at either low ($P_i = 0.310$, $\mu = 5.4$ cm/s, $\sigma = 4.80$) or high velocities ($P_i = 0.454$, $\mu = 30.6$ cm/s, $\sigma = 3.74$; Fig. 2). Although successful captures were relatively rare (five cases represented in Fig. 2 and Fig. 3a, b), they were invariably observed when one of these two tactics was used. The escape distance of crickets was somewhat reduced at low and high attack velocities (Fig. 3a) even though we observed a high interindividual variability. The velocity of spider attack was not related to the distance to the cricket (Fig. 3b).

EXPERIMENT 2: PISTON DESIGN

Methods

To reproduce in a controlled manner the different attack tactics and to understand the nature of associated stimuli, we used a circular piston (LAL35, Cedrat Technologies, Meylan, France) whose displacement kinematics was quantitatively as similar to that of attacking spiders as possible. The piston's front diameter was 0.8 cm versus 0.5–0.7 cm for spiders, leading to a Reynold's number around 150 versus 115 for spiders, at 30 cm/s (see Munson et al. 2005 for further explanation). Furthermore, the piston was displaced at a spider's height (0.2 cm) above the ground. The piston was connected to a high-speed controller (LAC-1, Cedrat Technologies, Meylan, France) driven by a computer. Both acceleration and velocity of the piston could be controlled with high precision (±4%) and the mean distance to reach a constant speed was set to 1 cm, as recorded for spiders (Fig. 1c).

To characterize the air flow generated by the piston's displacement we used a particle image velocimeter (PIV). PIV is a whole-flow-field technique providing instantaneous velocity vector measurements in a cross-section of a flow (Merzkirch 2001). The technique is nonintrusive and measures the velocities of micron-sized particles following the flow generated by the moving object in a laser sheet. In PIV, the velocity vectors are derived from subsections of the target area of the particle-seeded flow by measuring the movement of particles between two light pulses. The piston was placed in a sealed glass box

($20 \times 20 \times 10$ cm) seeded with 0.2-μm oil particles (Di-Ethyl-Hexyl-Sebacat, 0.5 L, TPAS, Dresden, Germany) using an aerosol generator (ATM 230, ACIL, Chatou, France). The laser of the PIV (NewWave Research Solo PIV 2, Nd:YAG, dual pulsed; Dantec Dynamics A/S, Skovlunde, Denmark) illuminated, through the glass, the flow produced by the piston's displacement in a plane perpendicular to the view of the camera. The laser sheet (width = 17 mm, thickness at focus point = 50 μm) was operated at low power (3 mJ at 532 nm) to minimize glare. A target area (17×30 mm) comprising ca. 20–30 droplets was then imaged on to the CCD array of a digital camera (Photron FastCam X1280 PCI 4K) using a Macro Lens (Nikon, AF Nikkor, 60 mm, f: 2.8). The focus of the laser sheet was at the centre of this target area. Every 200 μs, the CCD captured a light pulse in separate image frames (1280×1024 pixels). Once a sequence of two light pulses was recorded, the images were divided into small subsections which were cross-correlated with each other with a flow map software (Flow Manager 4.4. Dantec Dynamics A/S, Skovlunde, Denmark). The correlation produced a signal peak, identifying the common particle displacement. An accurate measure of the displacement (and thus of the velocity) was achieved with subpixel interpolation. We obtained a velocity vector map of the air flow displaced by the piston by repeating the cross-correlation for each interrogation area over the two image frames captured by the CCD camera. This was replicated five times for six piston velocities (5, 11, 15, 25, 40 and 50 cm/s).
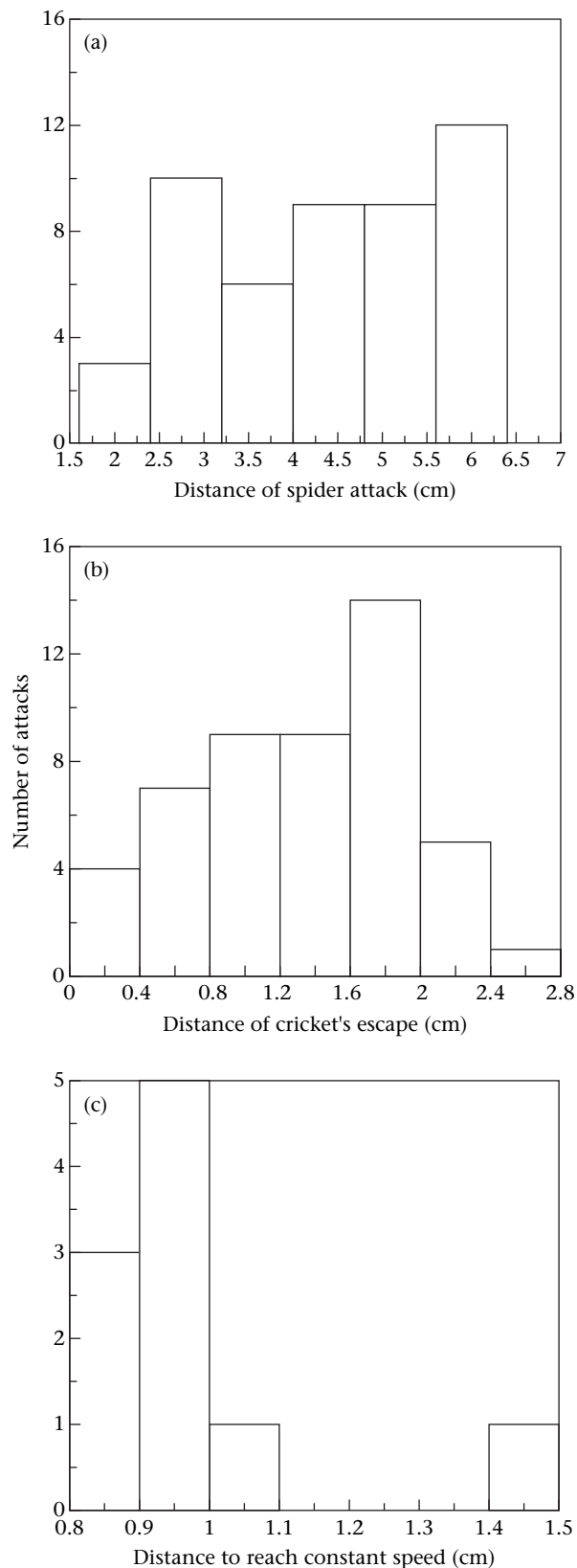
Results

PIV measurements provided the vector fields of the displacement of air particles generated by the piston (Fig. 4a). The velocity of air particles produced by the movement of the piston dropped very rapidly within the first few millimetres beyond the piston tip (Fig. 4b). This flow pattern is the one observed at constant velocity.

EXPERIMENT 3: RUNNING THE PISTON WITH CRICKETS

Methods

We used the piston approaching a cricket from the rear to mimic a spider's attack. To characterize with precision the cricket's reaction to the piston, we set up a bioassay where crickets were individually subjected to the piston approaching at various predetermined velocities, and measured their ensuing escape success. Crickets were placed on a circular stage that could be displaced in three dimensions and rotated. Once motionless, the cricket was placed rear-on 4.5 cm from the piston, the median distance at which spiders attack (Fig. 1a). After 5 s, the piston was launched and the cricket's escape behaviour was filmed at 55 frames/s under similar conditions as those presented in experiment 1. We focused on the velocity range measured for attacking spiders (5, 11, 15, 25, 40 cm/s; Fig. 2) but also increased the range beyond observed values (50 cm/s) to explore consequences on

crickets' performance. We tested 30 individuals at each piston's velocity in a randomized set-up to avoid adaptation to piston velocity. We scored successful escapes when the cricket's abdomen end was not touched by the piston.

Results

The median distance from the piston at which crickets initiated their escape behaviour was 1.6 cm (0.5–2.4 cm; Fig. 5), within the range of values found for crickets escaping from spiders (Fig. 1b). We found a hump-shaped relation between the piston's displacement velocity and the cricket's escape success (Fig. 5). The cricket's escape success was maximal for intermediate velocities (range 11–25 cm/s). Beyond these values, escape success decreased dramatically at very low (<8 cm/s) and very high (>33 cm/s) velocities. A comparison with Fig. 2 shows that more than 70% of fitted spiders' attacks occurred at these extreme velocities. The slow tactic of spiders nicely matched the velocity range for which cricket's escape success was very low. This matching was less clear for the fast attacks as an important proportion of spiders (18.3%) attacked crickets at intermediate velocities (25–30 cm/s) that still generated high escape success by the cricket. Attack velocities higher than 40 cm/s, although potentially very successful, were attained only once by spiders.

DISCUSSION

Bioassay Reliability

The antipredator behavioural response of air-sensing crickets and cockroaches has generally been studied by using loudspeakers for oscillatory predatory signals to mimic flying predators (Gnatzy 1996; Theunissen et al. 1996) and wind puffs for laminar ones (Westin et al. 1977; Tauber & Camhi 1995; Kanou et al. 1999). Although wind puff devices have proved successful to mimic the signal generated by a toad's tongue (1.2 cm/s, Camhi et al. 1978), they cannot be set up as precisely to match the kinematic characteristics (acceleration, velocity, head diameter) of most running predators of crickets, as our piston does. For this reason, our device represents a significant qualitative improvement over the traditional ones. However, air movements produced by a cylindrical piston with a flat leading surface are potentially different from the more complex movement generated by a running spider. To our knowledge, the air flow field at the front of a running arthropod has never been quantified. Ongoing full field measurements of air flows generated by dead

Figure 1. Quantitative characterization of the behavioural interaction between spiders and crickets. (a) Distribution of distances at which spiders initiated their attack ($N = 49$); (b) distribution of distances at which crickets initiated their escape ($N = 49$); (c) distribution of distances at which running spiders reached a constant velocity ($N = 10$). The number k of classes was calculated with the Yule formula (Zar 1998).
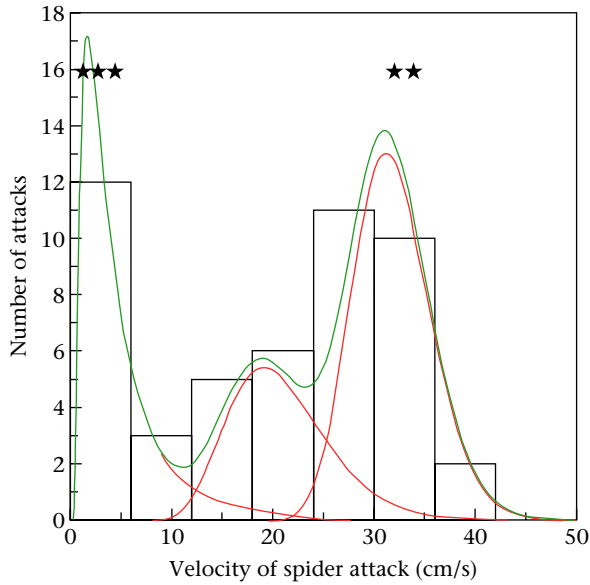
Figure 2. Distribution of displacement velocities of spiders attacking crickets ($N = 49$). The number k of classes was calculated with the Yule formula (Zar 1998). The curves represent the adjustment of the component distributions obtained by using a combination of a Newton-type method and EM algorithm. Asterisks indicate velocities at which the five successful captures occurred.

spiders pinned to the piston and by freely running spiders show a decreasing pattern of air flow in front of spiders very similar to that measured for the piston alone J. Casas, T. Steinmann & O. Dangles, unpublished data. This may be explained by the fact that air movements recorded far from running spiders are produced by the body trunk and not by the legs, as already suggested for running wasps by Gnatzy & Kämper (1990) using a microphone. As long as the front diameter of the piston is in the same range as that of the running predator, our device represents a good solution to mimic air flows produced by a wide array of predators of different size.

Attack and Escape Tactics

The usual description of predator foraging is to include tactics within an energy expenditure framework (Stephen & Krebs 1986). This predator-oriented view does not, however, include information on how prey defences influence both predator foraging behaviour and the dynamics of predator–prey interactions, and very little is known about this topic. Our results show that tactics adopted by spiders could be understood by merging physical and behavioural approaches using the interplay between the predator and its prey.

Figure 6 tentatively expresses the escape success of prey as a function of (1) the distance between prey and predator, (2) the velocity of the predator and (3) the detection level which is measured in units of predator signal. Based on the largest detection distances recorded in this study (2.4 cm at 15 cm/s) and our PIV measurements, the detection threshold could be fixed at ca. 0.1 cm/s air particle
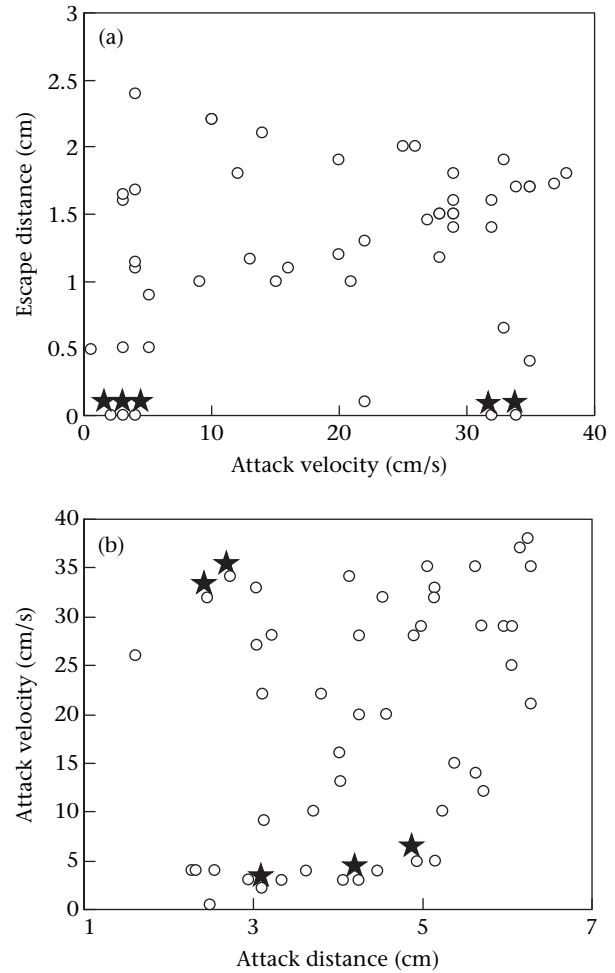

Figure 3. Scatterplots obtained from cricket–spider interactions: (a) escape distance versus attack velocity ($N = 49$); (b) attack velocity versus attack distance ($N = 49$). Asterisks indicate successful captures.

velocity (Fig. 4b), a value in agreement with the literature (Shimozawa & Kanou 1984). This threshold is symbolized in Fig. 6 by the horizontal dark red plane ($y = 0.1$ cm/s). The only signals that initiate escape are those that exceed the mechanical receptor threshold. In other words all subthreshold actions by the predator produce very low escape probabilities (dark red). At high attack velocities (40–50 cm/s), the cricket's latency to jump is too high (100–150 ms, Tauber & Camhi 1995) to allow an appropriate escape given the distance that separates it from the predator (on average 4.5 cm). This 100–150-ms delay means that the imperceptible distance to contact depends on the attack velocity. Together with attack velocity, the distance to the prey is therefore an important variable that determines the outcome of the attack. Although the impact of attack velocity was clearly demonstrated by our results, we found no relation between the spider's attack distance and the probability of catching its prey. Further investigation using the piston would be needed to quantify the relative importance of attack distance and attack velocity to the success of predators.
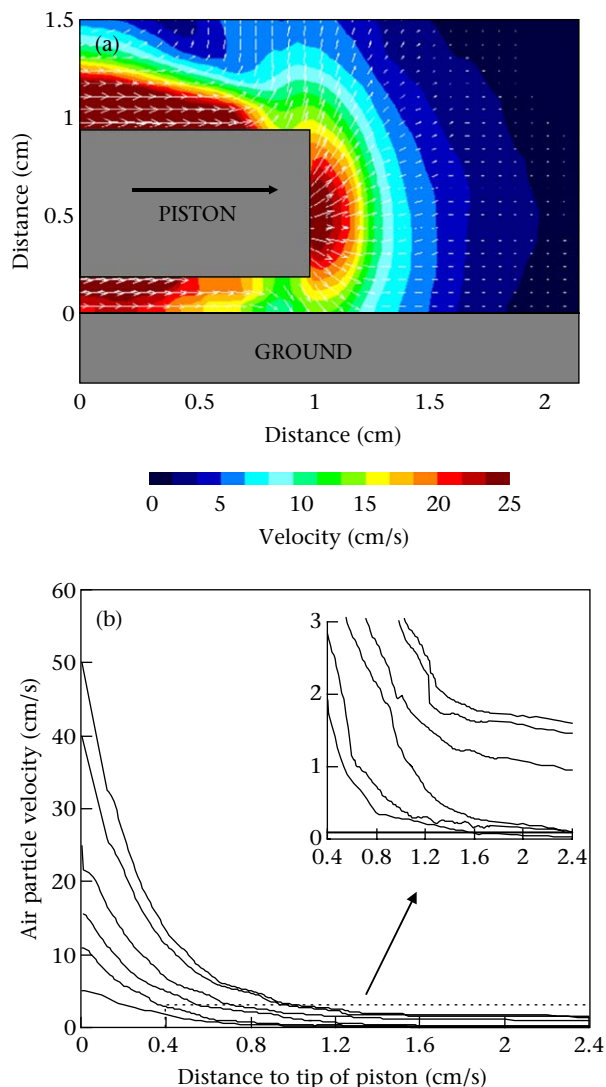
Figure 4. Particle image velocimeter (PIV) characterization of the field velocities generated by the piston. (a) Vector fields of displacement of oil particles in front of the piston (side view) calculated after PIV processing. The displacement velocity of the piston is 25 cm/s. Reynolds number = 130. (b) Velocity of air particles produced by the piston moving at different velocities (from bottom to top: 5, 11, 15, 25, 40 and 50 cm/s). The insert shows air particle velocity at higher magnification (0–3 cm/s).

Figure 5. (a) Mean ± SE escape success of crickets as a function of piston velocity ($N = 30$). Dotted line shows the spider's attack distribution curve from Fig. 2. (b) Distribution of response distances for crickets that successfully escaped ($N = 53$).

At low attack velocity, the cricket only needs to detect the predator 0.5 cm away to have time to escape. At this distance, the velocity of the air particles produced by the predator is about 1.5 cm/s, which is over 10 times the velocity needed for the cricket's response (Kanou & Shimozawa 1984). Although one might expect a large escape probability, the reverse is observed. This could be explained by the fact that at these velocities, the spider's movements could be lost within the background noise around the cricket because of natural air currents. Futhermore, a signal comprising little acceleration in air particle velocities from the source would be unlikely to be detected by the cricket. In addition to the two tactics (running at high and low velocity), the predator may use a sit-and-
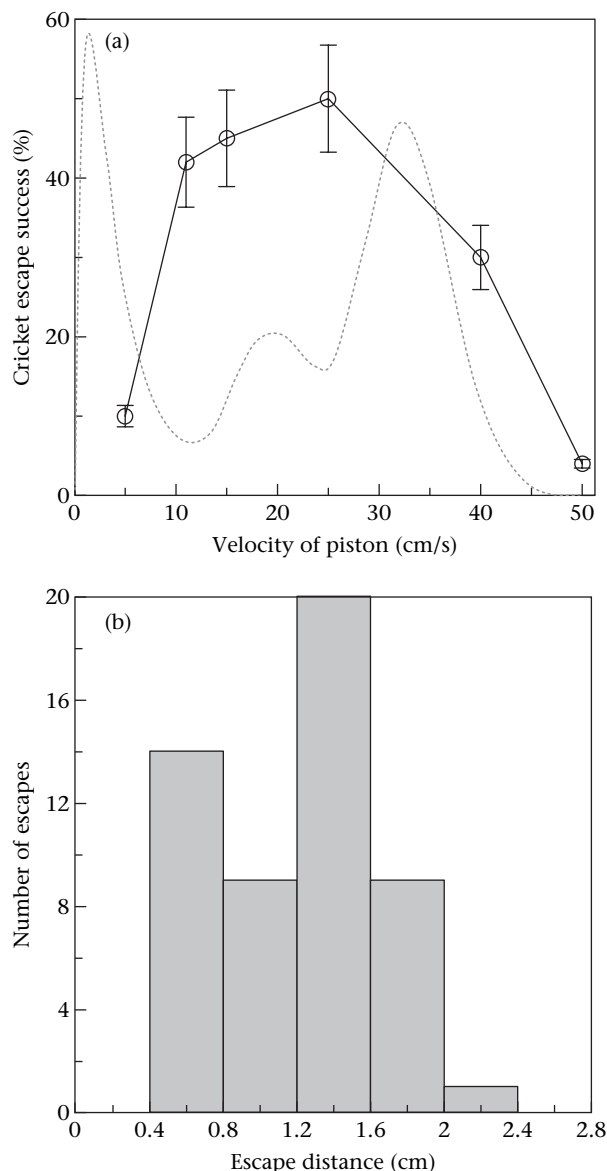
wait tactic: being very close to the prey ensures a successful strike whatever the attack velocity because the prey lacks the required time to react. The least profitable strategy for the predator is therefore to use intermediate attack velocities at intermediate prey distances and this is indeed what spiders appear to avoid (Fig. 1). However, we did not find any evidence that spiders are able to modify their attack strategy depending on the distance to the prey (Fig. 3b).

Although the general tactic of spiders (e.g. stationary versus wandering) has been clearly related to energy budget constraints (Ford 1977; Toft 1999), we believe that the detailed physical mechanics of both attack and escape have to be considered in building a more realistic framework for predator–prey interactions. Our results
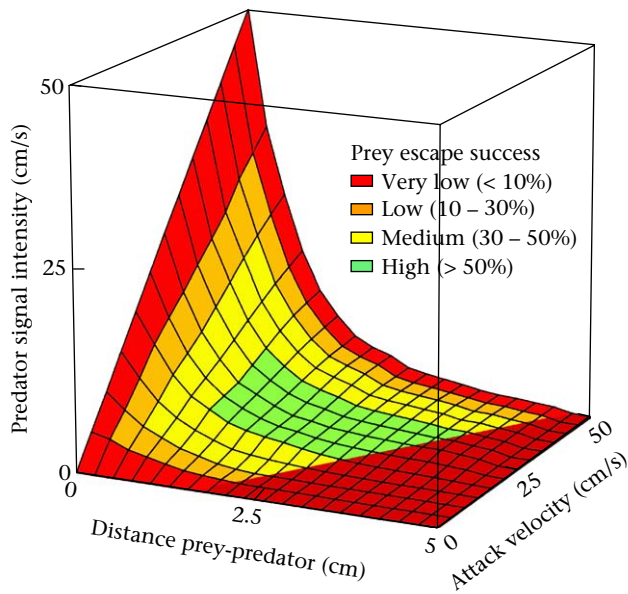
Figure 6. Synthetic graph of our results presenting the underlying mechanisms of prey–predator interactions at close range. Crickets perceive approaching predators only when their signal intensity (air movement velocity) reaches a certain level, set here at the level corresponding to the observed highest value of escape distance over different speed of attack (dark red plane). Above this level, their chances of escaping are restricted to only the intermediate region of predator attack velocity and distance to the prey (green). Crickets are easily preyed upon at lower velocity because predators produce very little air displacement (see text). At high attack velocity or at short distance, the predator overcomes the escape reaction of its prey despite the available information contained in the air movement. For the surface representation we used Akima's interpolation (Akima 1996).

are in general agreement with studies on two other predators that have been shown to overcome successfully orthopteroïd air-sensing systems. Indeed, Gnatzy & Kämper (1990) proposed that the running wasp, *L. niger*, is likely to adopt either a slow or a fast tactic to approach crickets. In contrast, the predatory strike of toads, *Bufo marinus*, is highly stereotyped and is an open loop reaction: the tongue protraction is always very rapid (fast tactic, Nishikawa & Gans 1996). Our conclusions could be extended to other predator–prey models. Speed modulation during attack has been reported in a wide array of vertebrate taxa such as fish (Wainwright et al. 2001), amphibians (Deban 1997), lizards (Vanhooydonck et al. 2002), birds of prey (Lind et al. 2002) and bats (Fullard 1987). Such a widespread occurrence in terrestrial, aerial and aquatic habitats suggests that predator–prey interactions are determined by common constraints which need to be investigated at a fine scale, from the perspective of both partners.

Acknowledgments

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