

Predatory behavior of the zebra spider, *Salticus scenicus* (Araneae: Salticidae)

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The zebra spider (*Salticus scenicus*), a small jumping spider, orients towards prey detected by its lateral eyes whenever the angle subtended by such prey exceeds 5.5°. The velocity of the prey is not involved in the determination of reactive distance, but only moving objects elicit orientation. The probability that orientation is followed by stalking is a function of both prey size and velocity, but the effects of these parameters on reactive distance for stalking were not determined. The zebra spider's stalk velocity declines progressively as it nears its (stationary) prey, and the probable optimality of this behavioral tactic is discussed.

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Le saltique harlequin (*Salticus scenicus*) petite araignée sauteuse, s'oriente vers une proie repérée au moyen de ses yeux latéraux, lorsque l'angle soustendu par la proie dépasse 5.5°. La vitesse de la proie n'influence pas la distance à laquelle l'araignée réagit, mais seuls les objets en mouvement entraînent l'orientation. La probabilité que l'orientation soit suivie d'une poursuite est fonction de la taille de la proie et de sa vitesse; cependant, les effets de ces paramètres sur la distance à laquelle l'araignée commence sa poursuite n'ont pas été déterminés. La vitesse de poursuite de l'araignée diminue progressivement lorsqu'elle s'approche de sa proie (stationnaire); on discute des avantages probables de cette tactique. [Traduit par le journal]

Introduction

The zebra spider (*Salticus scenicus*) is a jumping spider commonly observed hunting on the exterior walls of buildings on sunny days. Having detected a potential prey anywhere in its extensive visual field, the spider wheels around to face the object (a behavior referred to as "orientation"), and fixates it with the large anteromedian eyes. It is likely that retinal scanning movements are then carried out (Land 1969), enabling the spider to distinguish edible prey from conspecifics and inedible objects. A decision is made at this point either to attack the object, or to ignore it and resume searching. If the former, the spider stalks (=approaches) the prey, flattening itself to the substrate during the later stages of the approach. Stalks are usually oriented directly toward the prey, but if the prey is very large relative to the spider, the approach may be circular, ending behind the prey (also noted by Gardner 1965, in *Phidippus coccineus*, another species of jumping spider). Once very close to the prey, the spider attaches a drag line to the

substrate, and pounces at the prey with its forelegs extended anterolaterally. If the strike is successful the prey is bitten, rapidly immobilized, and masticated.

The objectives of the experiments described here were twofold. Firstly, an attempt was made to define quantitatively the characteristics of the stimulus situation which elicit orientation and stalking by zebra spiders. Characteristics examined were prey size, prey velocity, and distance between predator and prey. The data were collected to test the hypothesis that orientation occurs whenever the angle subtended by an object at the predator's eye exceeds some threshold level, as found for the mantid *Hierodula crassa* by Holling (unpublished data). This emphasis on reactive distance for orientation distinguishes the study from Drees' (1952) earlier attempt to define the key stimuli for prey capture in this species.

Secondly, filmed records of stalks were analyzed to determine the way in which stalk velocity varies with distance between predator and prey during the course of the stalk. A model of avoidance behavior by prey (Dill 1974) suggests that an optimally behaving predator should move progressively more slowly as it nears its prey.

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Methods

All of the spiders used in this study were males, about 8–10 mm in length. They were collected from buildings and fences at Black Creek Pioneer Village, Toronto, during a 5-day period in late June, 1974. Between experiments the spiders were housed individually in plastic petri dishes (supplied with water via a wick), and fed one vestigial-winged *Drosophila melanogaster* daily.

The apparatus shown in Fig. 1 was used to present model prey to the spiders. A bead, painted flat black, was towed upwards, adjacent to (but not quite touching) the pole, towards a spider situated at the top. The size of the bead could be varied, and its velocity controlled by a transformer attached to a 6-V electric motor. At the beginning of a test the spider was placed into the chamber on top of the pole. The inside walls of this chamber were coated with Fluon, a teflon-like material (C-I-L, Toronto, Ont.) which prevents climbing. To leave the chamber, the spider had no choice but to exit via a hole in the bottom, adjacent to the front of the pole. As the underside of the chamber bottom was also fluon-coated, the spider invariably ended up on the pole immediately in line with the path of the model prey. In addition, owing to the placement of the chamber exit, the spider also ended up facing about 45° from the vertical. Thus, prey could be presented at about the same angular position relative to the spider's midline in each trial. (According to Land (1971) the probability of an object at fixed distance being oriented to by jumping spiders of the genus *Metaphidippus* is greatest when the stimulus is presented 40–90° from the spider's midline.) Emerging from the chamber to the pole the spider usually remained stationary for a few seconds. It was during this period that the motor was turned on and the "prey," previously situated 12 cm below the top of the pole, began to move towards the predator. As soon as a recognizable orientation occurred the motor was stopped and the bead ceased to move. There was no obvious response to the sound of the motor.

The main experiment was conducted over a period of 2 days, after the spiders had been in the laboratory 6–12 days. The 80 spiders used were deprived of food for 3 days before the start of the experiment.

On day 1, 20 spiders each were presented with a 3.6-mm-diameter bead at velocities of 0.5, 1.0, 1.5, and 2.0 cm/s. The velocities were presented in random order during the course of the experiment (0900–1700 h). On day 2, 20 spiders each were presented with beads of 2.1, 3.6, 4.8, and 6.2 mm diameter, approaching at 1.0 cm/s. Owing to the difficulty of changing beads between trials, all of the trials with one "prey" size were presented sequentially, though the order of presentation of the four sizes was randomized (i.e. 20 × 3.6, 20 × 2.1, 20 × 6.2, 20 × 4.8). Every trial was filmed from the side with a Sankyo Super-8 camera and orientation distances measured from the films, using a PDQ II Motion Analyzer (Photographic Analysis Ltd., Toronto).

The same films were analyzed to determine the manner in which stalk velocity varied with predator-prey distance (estimated to the nearest 0.1 mm, aided by the 2-mm reference marks on the pole). However, since few stalks were observed in the main experiment, an additional 20 trials were conducted on day 3: 10 trials with the

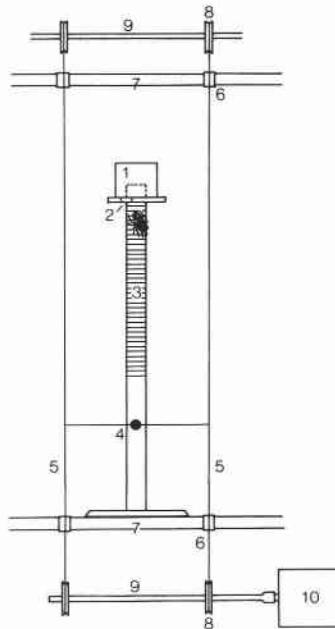


FIG. 1. Apparatus used to present model prey to the spiders. Legend: (1) chamber (coated with fluon) in which spider was placed at start of experiment; (2) hole in chamber floor allowing spider to move onto (3) 0.95-cm-diameter pole; (4) black bead towed by (5) lateral monofilament threads passing through (6) nylon bushings in (7) white plexiglass floor and ceiling of apparatus; (8) pulleys on (9) free axle (above) and drive shaft (below) attached to (10) 6-V electric motor.

2.1-mm prey at 1.0 cm/s, and 10 with a visually more complex "prey", a crude model of a fly (7.1-mm overall width) moving at same speed. The latter prey elicited nine stalks and these data were pooled with the data collected earlier for the purpose of analyzing stalk velocity.

Results and Discussion

Orientation

The size and velocity of the bead had no consistent effect on the probability that the zebra spider would orient towards it during its approach (Table 1). The overall proportion of orientations, compared with the results of other studies of salticid spiders presented with model prey (Drees 1952; Gardner 1966; Land 1971), indicates the adequacy of the present stimulus situation.

The distance from the prey at which orientation occurred was not significantly affected by model velocity ($p > 0.05$), lending support to the angular size hypothesis. The angle (α) subtended by the prey at the spider's eye at

TABLE 1
The effect of model size and approach velocity on percentage orientation,
and on the percentage of orientations which were followed by stalks

Day	Diameter, mm	Velocity, cm/s	Percentage orientation	Percentage stalks
1	3.6	0.5	35	33
		1.0	75	27
		1.5	50	30
		2.0	70	7
2	2.1	1.0	80	73
		3.6	45	0
		4.8	65	0
		6.2	75	0
Total			61.9	17.6

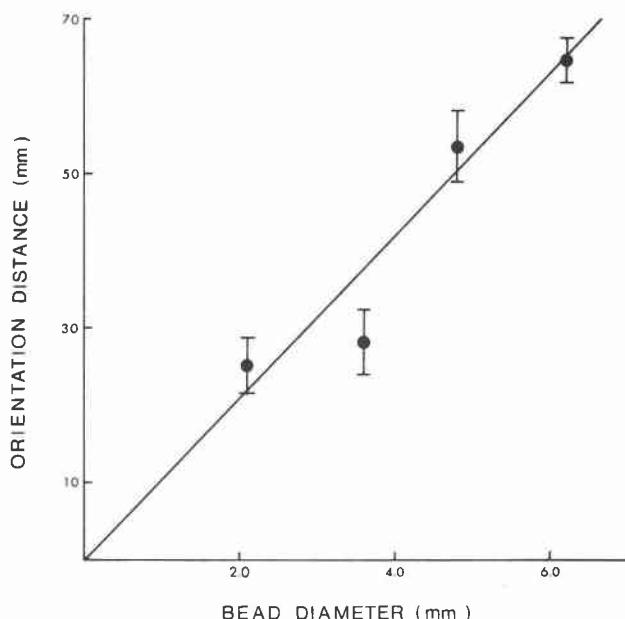


FIG. 2. Orientation distance (mean \pm standard error) of zebra spiders to model prey of various sizes.
All velocities combined. The regression ($y = 10.51x$) is significant at $p < 0.001$.

any particular distance (D) is

$$[1] \quad \alpha = 2 \arctan(S/2D),$$

where S = prey size. If the spider orients towards prey whenever α exceeds some threshold (α_{\min}) then (substituting α_{\min} for α and rearranging the above equation) reactive distance for orientation can be expressed as

$$[2] \quad D = (2 \tan 0.5\alpha_{\min})^{-1} S$$

and a regression of orientation distance on model size should have a positive slope and no

intercept. The equation best describing the observed data (Fig. 2) was

$$[3] \quad D = 1.24 + 10.21(S).$$

The slope is significant ($p < 0.001$), but the intercept is not significantly greater than zero ($p > 0.05$). The regression was therefore conditioned to go through the intercept, producing the equation

$$[4] \quad D = 10.51(S).$$

By setting the constant in eq. 2 equal to 10.51

the best estimate of α_{\min} was found to be 5.45° . The data therefore support the hypothesis that zebra spiders orient towards objects subtending at least 5.45° in their visual field. The velocity of the object is unimportant, but only moving prey elicit orientation, as previously reported for other salticids by Gardner (1964) and Land (1971).

Angle subtended by the prey has also been suggested as the stimulus determining orientation distance in mantids (Holling, unpublished data; Maldonado and Rodriguez 1972), and attack (including orientation) distance in the water strider *Gerris remigis* (Jamieson 1973), and rainbow trout (Ware 1973). The importance of angular size is also implicated in studies of orientation to prey by the toad *Bufo bufo* (Ewert 1970), the water strider *Velia caprai* (Meyer 1971), and the salticid spiders, *Metaphidippus harfordi* and *M. aeneolus* (Land 1971). Thus supra-threshold angular size appears to be a releaser for orientation behavior in a broad spectrum of predators. The reactive distance for orientation to prey is a function of hunger in the mantid *Hierodula crassa* (Holling 1966), the wolf spider *Pardosa vancouveri* (Hardman 1972), and the water strider *Gerris remigis* (Jamieson 1973), indicating that not all prey seen by these predators are responded to, i.e. the angular threshold is not simply a measure of (structural) visual acuity. Whether this is generally true of predators (especially vertebrates) is not known.

Sawfly (*Perga* sp.) larvae (Meyer-Rochow 1974), gerrid waterstriders (Jamieson 1973), the damselfish *Chromis cyanea* (Hurley and Hartline 1974), and other animals (Schiff 1965) are reported to show avoidance or other anti-predator responses to approaching predators whenever the angle subtended by the predator exceeds some threshold level. More carefully controlled experiments on zebra danios (*Brachydanio rerio*), however, suggest that predator velocity is also important in eliciting escape behavior (Dill 1974). Whether this is generally true is unknown, but its generality is assumed when discussing stalk velocity (below).

Stalking

The proportion of orientations which were followed by stalks of any duration was influenced by both model size and velocity (Table 1). In general the smaller and slower moving

prey were more likely to elicit stalking by the spider. Drees (1952) and Gardner (1966) also found that smaller models were more often stalked by salticids. The overall percentage of orientations leading to stalks (17.6%) is much lower than in *Phidippus clarus* presented with fruit flies (Gardner 1964). Thus, the stimulus used here, while adequate to release orientation, was perhaps not sufficiently realistic to allow the behavioral chain to continue. This is supported by the fact that 100% of the orientations to the simulated fly (day 3) were followed by a stalk. However, part of the explanation for this high proportion may lie in the fact that the spiders used on day 3 had been deprived of food an additional 24 h. Increasing deprivation time has this effect in other salticids (Gardner 1964, 1966).

Deprivation time differences cannot be used to explain the decrease from day 1 to 2 in willingness to stalk the 3.6-mm bead moving at 1.0 cm/s. Habituation is also an unlikely explanation, since the trials on any one spider were so widely spaced. Some unknown source of variation must be invoked. Similarly, on testing day 3 only 30% of the spiders which oriented to the 2.1-mm bead also stalked it (cf. 73% on day 2). If the results of all three experiments are combined the percentage of stalks towards beads moved at 1.0 cm/s were: 56, 17, 0, and 0 for the small through large beads respectively.

Having turned to face its prey, the spider can apparently assess size and distance independently. The decision to stalk, while size dependent, does not appear to be distance dependent. Moving the prey progressively closer to a non-stalking zebra spider seldom elicited a response: the spider usually stalked from the orientation distance or not at all. In contrast, Holling (unpublished data) found that the mantid has a reactive distance for stalking distinct from its awareness (orientation) distance, and that this distance is a dome-shaped function of prey size.

Pounces occurred on only eight occasions in the main experiment, and all of these were to the 2.1-cm bead which had been moved at 1.0 cm/s. These pounces represented 73% of the stalks towards that bead, and the average pounce distance was 14.5 mm. Similar pounce distances have been recorded for a variety of jumping spider species by Drees (1952), Gardner (1965),

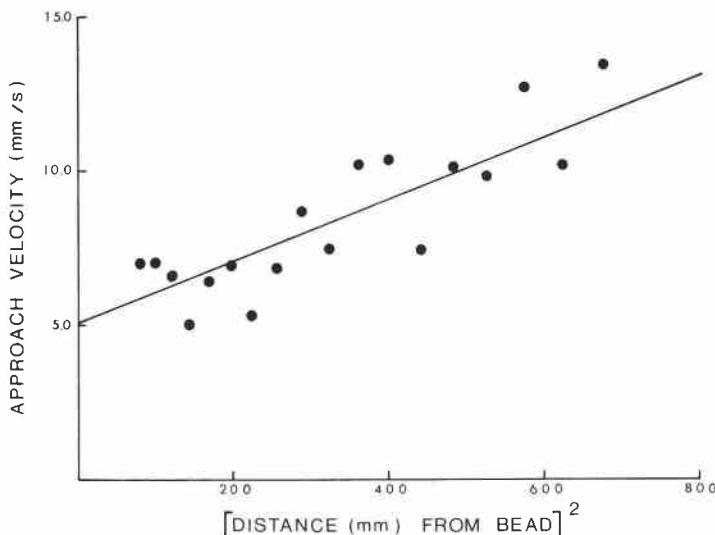


FIG. 3. Mean approach velocity of zebra spiders to model prey, as a function of distance separating them. The regression using all 327 individual data points ($V = 4.48 + 0.011D^2$) is significant at $p < 0.01$.

and Land (1969). Spiders which did not pounce often stalked closer to the prey than this. Sixty percent of the stalks directed towards the simulated fly on day 3 were terminated by a pounce (mean pounce distance = 11.6 mm).

Stalk velocity as a function of spider-model distance was measured in 35 stalks of varied duration. Eleven of these were towards 3.6-mm models (which had been moving at four different speeds), 14- to 2.1-mm models, and the remainder to the simulated fly. In addition these stalks were performed by the spiders after three different periods of deprivation (3, 4, and 5 days). Much of the variability in the data may be due to these confounding factors, but insufficient data existed for any one prey size - velocity - deprivation time combination, necessitating pooling.

Mean stalk velocity is plotted (Fig. 3) for all spider-bead distances for which 10 or more observations were available. The independent variable (distance) was squared to produce linearity, and a regression conducted. The equation best describing the 327 original data points is

$$[5] \quad \text{velocity} = 4.48 + 0.011(\text{distance})^2$$

with $p < 0.001$, supporting the contention that the zebra spider reduces its velocity as it gets progressively closer to its prey. Gardner (1964) has noted this anecdotally for *Phidippus clarus*, and there is a slight suggestion of such behavior

in Drees' (1952) paper on the zebra spider (see his Fig. 10).

The cyprinid fish *Brachydanio rerio* responds to approaching predators whenever the angle subtended at its eye by the predator increases at a rate greater than some threshold level, and there are indications that this may be generally true for prey species (Dill 1974). Rate of change of visual angle (looming rate) may be calculated from the equation

$$[6] \quad d\alpha/dt \text{ (rad/s)} = 4VS/(4D^2 + S^2).$$

Since spider velocity (V) is known for each distance (D) it is possible to calculate the $d\alpha/dt$ signal perceived by the prey during the spider's approach, if spider size (S) is known. This was assumed to be the spider's maximum diameter in front view (estimated to be 7 mm). Rate of change of visual angle was then calculated for spider-prey distances from 9 to 26 mm, with either decreasing spider velocity (eq. 5) or a constant high velocity corresponding to that measured at 26 mm.

The results (Fig. 4) clearly demonstrate that a spider reducing its velocity during the stalk presents to the prey a slower rate of increase of $d\alpha/dt$ than would a spider stalking at constant high velocity. High velocities are allowable early in the stalk since $d\alpha/dt$ is small, but decreasing velocity as the prey is approached forestalls the production of a $d\alpha/dt$ signal above the prey's assumed threshold level, i.e. the level at which

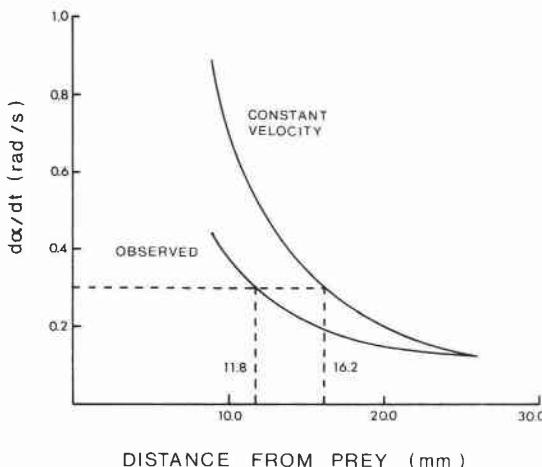


FIG. 4. The looming signal ($d\alpha/dt$) presented to a prey by a spider approaching at a constant velocity (equal to that observed 26 mm from the prey) and by one approaching with a velocity decreasing as observed in Fig. 3. A prey with a $d\alpha/dt$ threshold of 0.3 rad/s could be approached to 11.8 mm by the latter spider but only to 16.2 mm by the former.

it initiates escape behavior. Crouching down by the spider during its approach may further decrease the rate of growth of $d\alpha/dt$ by decreasing apparent size, but this behavior has not been considered in the present analysis. If the prey of the zebra spider do indeed take flight when $d\alpha/dt$ exceeds some threshold level, then the observed behavior of the spider allows it to get closer to its prey before it must pounce than would be the case if it moved at constant high velocity (Fig. 4). This would obviously be important if pounce success is an inverse function of initiation distance, as has been reported for the final lunge of the largemouth bass (Dill 1973). The observed behavior, then, is suspected to be optimal for the predator, given its own behavioral limitations and the escape mechanism of the prey. Whether or not the tactic is energetically optimal will depend on the importance of handling time in determining the rate of prey capture; slowing down during the approach requires more time to be expended in the capture of any one prey. A more detailed study of predator and especially prey behavior, and of foraging energetics (a strategic approach), is suggested by these preliminary results.

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