

LOCATION OF SUCCESSFUL STRIKES ON PREY BY JUVENILE CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT. Second-instar crab spiderlings *Misumena vatia* (ca. 0.6 mg) that had never previously fed made killing attacks on pomace flies *Drosophila melanogaster* (ca. 1.0 mg) in direct proportion to the surface areas of the flies' body parts: abdomen, 50%; thorax, 29%; head, 20%. They retained this pattern over their next six encounters with these flies. They also attacked the different surfaces of these body parts (front, side, above, below, behind) with a frequency predicted by the respective areas of these surfaces. All of the spiderlings tested more than once successfully attacked prey on more than one body part. Fifth and sixth-instar *Misumena* (ca. 7–15 mg) attacked small (4 mg) syrphid flies *Toxomerus marginatus* more frequently on the head than the second instars attacked *Drosophila* heads. This difference may result from subsequent experience, greater activity of the syrphid flies than the *Drosophila*, or maturation of the spiders.

A wide variety of animals employ a sit-and-wait predatory strategy, ranging from spiders and insects to lions (Curio 1976; Morse 1980). Sit-and-wait predators depend primarily on prey coming to them and consequently will encounter many of these prey either head-on or tangentially, even though some of these predators may orient to their prey and even pursue them for short distances. These predators often increase their proficiency with experience (Bailey 1985; Cloarec 1991), which may result from the development and refinement of a particular repertoire (Papaj & Prokopy 1989), and may include new prey species as the predator grows, or as the season changes (e.g., Erickson & Morse 1997). The body part (head, thorax, abdomen) of the prey struck by the predator may form an important part of a developing repertoire exhibited by sit-and-wait predators.

Little information exists on the initial part of the body struck successfully by spiders, including classic sit-and-wait predators (Foelix 1996a, 1996b), despite the oft-cited "neck-bites" found in general sources (e.g., Bristowe 1958; Main 1976). To my knowledge, information on strike sites does not exist for naive spiderlings of any species making their first kill. Spiderlings are excellent subjects for such an investigation, because they can be easily obtained in large numbers and can be easily run in enclosures using readily available prey.

In this paper I report the body parts of prey, wild-type pomace flies *Drosophila melanogaster* Meigen, successfully struck by just-emerged, second-instar crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) making their first captures, as well as the body parts successfully attacked in several subsequent captures by these spiderlings. *Drosophila* approximate the size and activity patterns of small Diptera encountered by the spiderlings in the field and often constituting their first captures (Morse 1993). I then compare these results with those of fifth and sixth-instar *Misumena* attacking small syrphid flies *Toxomerus marginatus* (Say), an important prey item of older *Misumena* in the field. These results provide important insights into the development of prey-capture behavior in *Misumena* and also provide the basis for future comparisons with other species.

METHODS

I obtained all spiders and syrphid flies from old fields and roadsides in South Bristol, Lincoln County, Maine in August of 1995 and 1996, and *Drosophila* came from wild-type laboratory stocks. All second-instar spiderlings used in this study had emerged from their egg sacs within the preceding two days at the time of their first observation. The egg sacs themselves had been collected from the field shortly before emergence. Laying dates

of these clutches were known, so approximate emergence dates could be calculated. Middle-instar spiders and syrphid flies were collected from goldenrod (*Solidago* spp.) flowers, which both the spiders and the flies frequented during August. All spiderlings were weighed before their first experimental run, and their similar masses (0.4–0.7 mg; Morse 1993) ensured that they had not cannibalized their sibs [a rare event occurring in less than 10% of the broods (DHM unpubl. data)], and, therefore, had not previously fed. The spiderlings were tested seven times, at three-day intervals. Since a few were lost during handling, a few died, and most refused to feed on one or more occasions, I obtained the maximum seven data points for only four of the 32 individuals run in this protocol.

I placed approximately 10 *Drosophila* (ca. 1.0 mg, 3 mm body length) in a petri dish (6 cm diameter) and then added a second-instar spiderling to the dish. Although a high-density setting, this density is frequently approximated when just-emerged, second-instar *Misumena* recruit onto goldenrod inflorescences that contained large numbers of small dance flies (Empididae) (Morse 1993). The *Drosophila* were lightly chilled to immobilize them sufficiently for convenient handling, and then allowed to recover before adding the spiderling. I recorded the body part where the spiders first successfully struck their prey (head, thorax, abdomen) and the surface of the body part they struck (anterior, lateral, dorsal, ventral, and posterior). As soon as a spiderling captured either a *Drosophila* or syrphid fly, I viewed it under a dissecting microscope to verify the site of the successful attack. Since these individuals were carefully observed for up to 30 min, I missed few predation events. The close observations ensured that none of the spiderlings shifted their positions on their prey before being recorded. Spiders often reposition their prey subsequent to capture (Foelix 1996a), necessitating this close attention. These spiderlings required a few minutes to shift from the original kill site (pers. obs.), although attention to obtaining original kill sites made it impossible to record exact shift times as well.

I calculated expected frequencies of attacks on the head, thorax, and abdomen as the relative surface area of each of these body parts; excluding the posterior surface of the head,

anterior and posterior surfaces of the thorax and anterior surface of the abdomen; surfaces largely occluded from strikes by surrounding structures. I calculated the areas from measurements of length and width of the head and thorax, estimating them to be cylinders. The anterior surface of the head was calculated as the area of a circle. The anterior part of the abdomen, back to the point at which it tapered, was also treated as a cylinder, and the remaining posterior part as a cone. This calculation assumed that the spaces separating head and thorax, and the thorax and abdomen, were too narrow to permit a successful strike and deleted these surfaces from the areas calculated. Since only four of 148 successful attacks struck these sites between the body parts, the criteria seem appropriate.

I also gathered similar data on the prey capture of small (ca. 4.0 mg, 5 mm; Morse 1979, 1998) syrphid flies *Toxomerus marginatus* by older, wild-caught, juvenile female *Misumena* weighing 6.9–15.6 mg (probably fifth and sixth instars). Relative proportions of area on the three body parts of *Toxomerus* were calculated as for *Drosophila*. These observations were made in 7-dram vials (5 cm long, 3 cm diameter), which also permitted me to observe initial capture sites. However, I did not record the part of the head, thorax, or abdomen where the syrphids were struck by the spiders.

RESULTS

Second instars attacking *Drosophila*.—In their first run, naive second instars made more of their first killing attacks to the abdomen than to the thorax or head of *Drosophila*, and more killing attacks to the thorax than to the head (abdomen > thorax > head) (Table 1). This distribution of killing attacks to the different body parts did not differ significantly from the number predicted as a consequence of the different surface areas of these body parts (Table 1) ($G = 1.09$, $df = 2$, $P > 0.5$ in a G -test), since the surface area of the abdomen considerably exceeded that of the thorax, which in turn exceeded that of the head (Table 1). Likewise, the sites of attack in the original trial and in the mean of the combined subsequent trials did not differ (Table 1) ($G = 0.36$, $df = 2$, $P > 0.8$ in a G -test). Neither did the original and last trials (Table 1) differ in a G -test ($G = 0.90$, $df = 2$, $P > 0.5$). In fact, comparisons of only two pairs of trials (2 and

Table 1.—Successful strikes (kills) of *Misumena vatia* on body parts of prey and percentage of total surface area of each body part. Predicted number of strikes (in parentheses), based on percentage of total surface area.

	Head	Thorax	Abdomen
<i>Drosophila</i> strikes			
First run	5 (4.4)	7 (6.9)	12 (12.7)
Second run	3 (5.4)	10 (8.3)	16 (15.3)
Third run	4 (5.2)	14 (8.0)	10 (14.8)
Fourth run	7 (3.9)	5 (6.0)	9 (11.1)
Fifth run	5 (3.2)	6 (4.8)	6 (9.0)
Sixth run	6 (2.0)	2 (3.2)	3 (5.8)
Seventh run	6 (3.3)	5 (5.2)	7 (9.5)
% surface area	18.6	28.6	52.8
<i>Toxomerus</i> strikes			
First run	15 (5.8)	12 (8.9)	4 (16.3)
% surface area	17.5	28.2	54.3

6, 3 and 6) differed at $P < 0.05$ (2 vs. 6: $G = 8.21$, $df = 2$, $P < 0.02$ in G -test; 3 vs. 6: $G = 6.84$, $df = 2$, $P < 0.05$ in same test), and their validity is highly suspect, because of the small sample sizes in two cells of Trial 6. Further, neither comparison is significant when a sequential Bonferroni adjustment (Rice 1989) is applied to accommodate for the multiple comparisons carried out. Successful strikes in runs 2–7 continued to follow the order abdomen > thorax > head in most instances, consistent with the different surface areas of the three body parts. Thus, no significant shift in sites occurred over the period during which these spiderlings killed their first several prey.

None of the spiderlings specialized strongly on a particular body part; in fact, none of the 29 individuals tested more than once confined their kills to a single body part ($P < 0.001$ in a binomial test). The pattern of attack thus showed little sign of specialization, at the individual or population level.

As no clear shifts in killing patterns emerged in the analysis of consecutive kills, I pooled the data from the different runs in order to establish how the spiderlings directed their killing attacks to the different surfaces of the body parts (Table 2). With 15 total surfaces recognized (Table 2), the sample of kills from any single run or pair of runs was not large enough to test statistically. The results can, however, establish where a predator most frequently attacks a prey species, an aspect that may serve to drive selection of prey-capture techniques of the predator, and corresponding selection on the prey species.

The spiderlings showed little tendency to capture prey by striking between the body parts, with only four such successful strikes, these being directed to the rear of the head (3) and the rear of the thorax (1). Deleting the areas of these four surfaces largely covered by adjacent body parts, successful attacks were carried out to the 11 remaining surfaces of the three body parts at rates that did not differ from the predicted ($G = 10.81$, $df = 10$, $P > 0.3$ in a one-sample G -test). Thus, the areas of the various surfaces of the different body parts also accurately predicted the rates at which these sites were successfully struck.

Later instars attacking syrphid flies.—Middle-instar spiders successfully struck *Toxomerus* on the head and thorax far more often than predicted by chance, based on the respective surface areas of the body parts (Table 1) ($G = 31.13$, $df = 2$, $P < 0.001$ in a G -test). This tendency differed significantly from that of the second instars capturing their first prey item ($G = 12.42$, $df = 2$, $P < 0.01$ in a G -test). I did not record the surfaces of the body parts struck that resulted in kills by these middle-instar spiders.

DISCUSSION

These spiders must be able to capture a broad range of prey over their lifetimes, both

Table 2.—Strikes of second-instar *Misumena vatia* on different surfaces of *Drosophila* body parts. Predicted number of strikes in parentheses, based on percentage of total surface area.

Body part	Surface area				
	Front	Side	Above	Below	Behind
Head	12 (8.4)	8 (9.2)	4 (4.6)	9 (4.6)	3 —
Thorax	0 —	24 (20.5)	9 (10.3)	15 (10.3)	1 —
Abdomen	0 —	19 (27.8)	9 (13.9)	22 (13.9)	13 (20.5)

as a consequence of their change in size and with the progression of the season. Opportunities will also differ with the habitat, and these sit-and-wait predators will also experience changes associated with the flower hunting sites experienced here. It is thus not surprising that the spiderlings do not exhibit a highly programmed repertoire upon initial experience with prey. Species with such varied demands often learn to perfect foraging repertoires appropriate to their context; where parental care is involved, this procedure often involves extensive information passed on from parent to offspring (e.g., Altmann 1998); where not, extensive trial-and-error may be required (e.g., Heinrich 1976).

It is of interest that the spiderlings did not exhibit any clear pattern of change in surfaces struck over seven runs. Clearly, they caught these prey with little difficulty, mostly capturing a *Drosophila* in a few seconds to several minutes (DHM pers. obs.), and thus they probably never accumulated information that favored shifts in prey-capture patterns. These spiderlings' high success rates differ markedly from that of second instars attacking *Toxomerus* flies (Erickson & Morse 1997), or that of adults on bumble bees *Bombus* spp. (Fritz & Morse 1985), both far more formidable prey than *Drosophila*. Although the conditions experienced in this experiment clearly differ from many situations experienced by novice foragers, such conditions are not unusual for naive *Misumena* spiderlings, as they typically recruit onto goldenrod inflorescences, which have wide, platform-like surfaces and, often, dozens of dance flies of 0.7–0.8 mg mass within a single small group of inflorescences. These flies are slow-moving and show little sign of responding evasively to the spiderlings (Morse 1993), and spiderlings probably experience little selection to position their site of attack more precisely on these small prey.

The tendency of the spiderlings to approximate predictions of strike sites based on surface areas of the prey, and the stronger orientation to the anterior part of the body in the larger spiders, suggest that the spiders modify their patterns somewhat with experience, although maturation could also account for the change. The failure of spiderlings to confine their activities to one body part or another may simply be a consequence of the substan-

tial proportions of prey taking trajectories that place them both face-on and lateral to the spiders, as occurs routinely when foraging on flowers in the field (Morse 1986). The older spiders probably also encounter higher proportions of prey moving directly toward them, as frequently occurs with active prey (Curio 1976), which would further enhance the probability of striking the anterior parts of a prey item. Although the spiders attacked these flies in laboratory containers rather than on flowers, the frequency in the field seems unlikely to change greatly because of the spiders' primary foraging strategy of waiting for such insects to approach them.

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LITERATURE CITED

- Altmann, S.A. 1998. Foraging for survival. Univ. of Chicago Press, Chicago.
- Bailey, P.C.E. 1985. "A prey in the hand", multi-prey capture behaviour in a sit-and-wait predator *Ranatra atra* (Heteroptera: Nepidae), the water stick insect. *J. Ethol.*, 3:105–112.
- Bristowe, W.S. 1958. The world of spiders. Collins, London.
- Cloarec, A. 1991. Handling time and multi-prey capture by a water bug. *Anim. Behav.*, 42:607–613.
- Curio, E. 1976. The ethology of predation. Springer Verlag, New York.
- Erickson, K.S. & D.H. Morse. 1997. Predator size and the suitability of a common prey. *Oecologia*, 109:608–614.
- Foelix, R.F. 1996a. How do crab spiders (Thomisidae) bite their prey? *Rev. Suisse Zool.*, hors serie:203–210.
- Foelix, R.F. 1996b. *Biology of spiders*, 2nd ed. Oxford Univ. Press, New York.
- Fritz, R.S. & D.H. Morse. 1985. Reproductive success, growth rate and foraging decisions of the crab spider *Misumena vatia*. *Oecologia*, 65:194–200.
- Heinrich, B. 1976. The foraging specializations of

- individual bumblebees. *Ecol. Monogr.*, 46:105–128.
- Main, B.Y. 1976. *Spiders*. Collins, Sydney.
- Morse, D.H. 1979. Prey capture by the crab spider *Misumena calycina* (Araneae: Thomisidae). *Oecologia*, 39:309–319.
- Morse, D.H. 1980. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge.
- Morse, D.H. 1986. Predatory risk to insects foraging at flowers. *Oikos*, 46:223–228.
- Morse, D.H. 1993. Some determinants of dispersal by crab spiderlings. *Ecology*, 74:427–432.
- Morse, D.H. 1998. The effect of wounds on desiccation of prey: implications for a predator with extra-oral digestion. *Oecologia*, 115:184–187.
- Papaj, D.R. & R.J. Prokopy. 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Entomol.*, 34:315–350.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, 43:223–225.

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