2010. The Journal of Arachnology 38:309–312

Effect of prey size on growth of newly emerged crab spiderlings *Misumena vatia*

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Abstract. Capturing unusually profitable prey early in life potentially enhances one's future fecundity and survival. Newly emerged crab spiderlings *Misumena vatia* (Araneae: Thomisidae) occasionally capture prey that greatly exceed them in size. I attempted to evaluate what if any long-term advantage these kills provided by presenting naïve, just-emerged spiderlings with syrphid flies *Toxomerus marginatus* that exceeded the initial mass of the spiderlings six-fold, a prey that the spiderlings occasionally captured in the field. A second group of spiderlings received a single syrphid initially and subsequently a single fruit fly *Drosophila melanogaster* every other day, and a control group received a fruit fly every other day. The few spiderlings that regularly captured the syrphids gained significantly more mass than the other groups. Individuals taking an initial syrphid and then fruit flies did not gain more mass than controls fed on solely on fruit flies. Neither did a group of spiderlings followed in the field nor a small group of individuals fed multiple fruit flies every other day in the laboratory differ in growth rates from the syrphid + fruit fly or single fruit fly groups. Thus, capture of a single bonanza prey does not provide the spiderlings with a significant advantage over those that did not obtain this reward, and in the field they probably do not manage to duplicate the capture success of the surviving members of the syrphid-only group.

Keywords: Dance fly, foraging, large prey, starvation, Thomisidae, *Toxomerus*

An individual's first foraging efforts often are inefficient, and without rapid improvement may result in a high probability of death. This problem may exist for a wide range of animals, from those provisioned by their parents as newborns and early juveniles (e.g., altricial birds: Lack 1966) to those that must forage for themselves from birth (e.g., many invertebrate species: Heinrich 1979; Morse 2000). If individuals must forage for themselves from the very start, innate traits will probably play a dominant role in governing initial responses. Still, since many animals, especially predators, potentially feed upon a wide variety of food items, an entirely innate response may not serve them well. Although naïve young may have little prior basis for discrimination (Persson & Brönmark 2009), it has become increasingly clear that the young of some species can rapidly modify their behavioral traits in a way that improves their performance in tasks such as foraging and hunting (Abramson 1994; Morse 2000).

Crab spiderlings *Misumena vatia* (Araneae: Thomisidae) (Clerck 1757) newly emerged from their natal nest sacs will attack a wide variety of prey, usually insects, on the flowers they occupy as hunting sites (Morse 1986). In response to the initial capture of a fruit fly *Drosophila melanogaster*, spiderlings may change their frequency of orientation and success of capture in subsequent attacks (Morse 2000). Spiderlings encounter a wide variety of insects on late-summer and early-autumn flowers in their natural habitat, ranging from ones far too large to capture (e.g., social bees) to easily captured ones (e.g., thrips, dance flies). Though at ca. 0.6 mg they obviously cannot capture the largest items with which they come in contact, they occasionally do take impressively large prey ranging up to several times their own body mass (Erickson and Morse 1997). It is thus of considerable interest to ask whether these endeavors are profitable in the long term (Christensen 1996; Sih & Christensen 2001) and if not, whether they are subsequently excluded from the foraging repertoire.

One such common visitor to these flowers that the spiderlings occasionally capture is the syrphid fly *Toxomerus marginatus*, which averages 4.0 mg (Erickson and Morse 1997; Morse 1998), over six times the mass of a newly-emerged spiderling. In fieldwork with these spiderlings I have observed such captures often enough (three in the past five summers of intensive fieldwork) to establish that they represent highly unusual, but by no means unique, events among spiderlings hunting on flowering goldenrod *Solidago* spp. (Asteraceae) inflorescences in late summer. The question thus arises, given the uncertain nature of prey capture at flower sites, how much advantage does such an apparent bonanza bestow on a just-emerged spiderling? In addition to lowering the danger of starvation (see Vogelei and Greissl 1989; Morse 1993a), a large capture might shorten the overall development time to adulthood and allow an individual to reach a greater size (Beck and Connor 1992) with potential enhanced fecundity (Morse and Fritz 1982). In contrast, poor early hunting success may lower any or all of these variables. Although some species can compensate for poor early success (Arendt 1997; Jespersen & Toft 2003), it may impose long-term fitness costs, such as decreased survival or reproduction (Metcalfe & Monaghan 2001).

I thus tested the question: does the initial capture or regular capture of extremely large prey items, here *T. marginatus*, provide newly emerged *M. vatia* spiderlings with significantly greater early gains in mass than those provided entirely by small prey? The results presented here took place during the first month following the spiderlings' emergence from their nest sacs. Although they represent only the first part of a juvenile's life, early success should enhance future fitness (Morse 2000).

METHODS

I carried out this work at the Darling Marine Center, South Bristol, Lincoln County, Maine (43.57°N, 69.33°W), in a 3.5 ha field containing several forbs that provide hunting sites for the spiderlings. During the period of study in August (2003–2008), large numbers of flowers, primarily goldenrods *Solidago* spp., bloom in this field, which I have described in detail elsewhere (Morse 2007). Voucher specimens from this population of *M. vatia* have been deposited in the American Museum of Natural History, New York.

To test whether they would gain additional mass under the most favorable of possible circumstances, I provided naïve, newly-emerged *M. vatia* spiderlings with one of three feeding regimes: regular access to the syrphid *T. marginatus*, a single *T. marginatus* followed by regular access to fruit flies, and regular access to fruit flies only. Juvenile *M. vatia* will readily progress through several instars with fruit flies fed on standard media (Carolina Biological Supply, Burlington, North Carolina) (D.H. Morse 2000, unpublished data), although most females experience difficulties maturing on this diet (see Uetz et al. 1992; Mayntz and Toft 2001).

Spiderlings were housed in 7-dram vials (5 cm high × 3 cm diam.) at ambient temperature and day-length and offered a prey item every other day. Earlier efforts (Morse 2000) demonstrated that the spiderlings would not regularly accept prey more frequently than every second or third day. Clearly the capture of a syrphid by a newly emerged individual is a prodigious feat, even within the artificial confines of a small vial. Relatively few of these individuals captured syrphids within a two-day period. I only retained the spiderlings that initially captured a syrphid and released the unsuccessful individuals into the field. Spiderlings that captured syrphids were randomly assigned to either a pure syrphid diet or a fruit fly diet. I compared the success of spiderlings assigned to a pure syrphid diet with the success of all spiderlings presented with syrphids for the first time. Control spiderlings, drawn from the same pool of individuals as those exposed to the syrphids, also received one fruit fly every other day. I repeated these efforts until I had obtained *n*'s of approximately 20 for each of the three groups. Additionally, I ran a small sample of 10 spiderlings that had initially captured a syrphid with several fruit flies every other day.

I maintained the spiderlings in these feeding trials for one month, recording molts and mortality and subsequently comparing the final masses of individuals from the three main conditions with a one-way ANOVA, followed by Tukey-Kramer tests. I subsequently compared the syrphid + fruit fly and syrphid + several fruit flies samples with a two-tailed *t*-test for the difference between two means.

Although artificial, these conditions provide insight into the most advantageous conditions that the spiderlings could experience in the field. To provide a realistic comparison, I followed a set of 10 spiderlings for one month on goldenrod (*Solidago canadensis*), regularly weighing these individuals. Goldenrods are abundant herbaceous perennials that form large inflorescences of tiny flowers, those of *S. canadensis* being plume-like in character. Observations and measurements of these spiderlings ended when the goldenrod floral substrate had almost completely senesced, resulting in dispersal of the spiderlings.

To provide a natural comparison with the laboratory feeding regime, I censused insect visitors to several goldenrod inflorescences during mid-day (11:30–13:30 h) at several times over the flowering season. In addition to the syrphids, large numbers of a small dance fly (Empididae) frequented the site (Morse 1993b). The spiderlings readily captured these 0.8–0.9 mg flies and fed exclusively or nearly exclusively on them at this time; thus, their diet bore considerable similarity to the laboratory spiderlings' fruit fly (ca. 1 mg) diet.

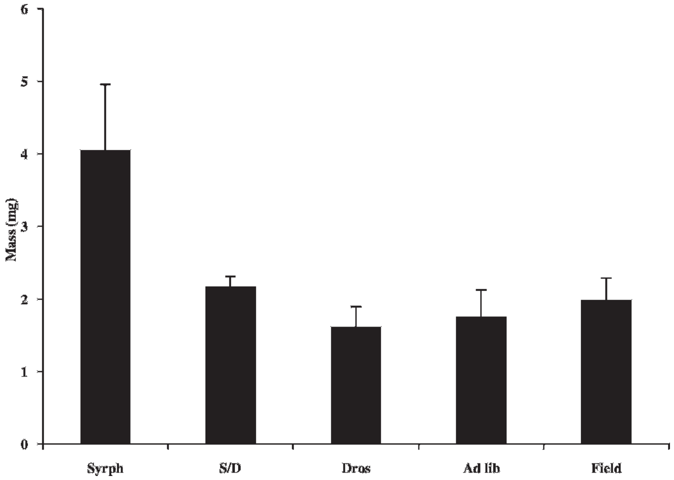

Figure 1.—Gains in mass (mg) of newly emerged spiderlings *Misumena vatia* that survived one month + 1 SE. Syrph = fed only one syrphid fly *Toxomerus marginatus* every other day, S/D = fed initial syrphid and then one *Drosophila melanogaster* every other day, Dros = fed one *Drosophila* every other day, Ad lib = five or more *Drosophila* every other day, Field = free-ranging in field on goldenrod *Solidago canadensis* inflorescences.

RESULTS

Gains in mass differed significantly among the three basic laboratory feeding regimes (Fig. 1: $F_{2,61} = 18.42$; $P < 0.0001$ in a one-way ANOVA). Individuals that fed only on syrphids weighed significantly more than those taking an initial syrphid and then fruit flies or from those presented only fruit flies (Tukey-Kramer tests, $P < 0.05$). The mass of the latter two groups did not differ significantly from each other ($P > 0.05$, same test). However, the syrphid-only group also experienced much higher mortality rates than the other groups (Fig. 2: $G_2 = 18.41$, $P < 0.001$ in a *G*-test of independence), due to the failure of several individuals to capture these large prey on a regular basis, as opposed to the fruit fly only or syrphid + fruit fly groups. Thus, the mortality rate obtained for the syrphid-only group is likely to be conservative, since individuals that did not capture syrphids in the first place would seem unlikely to capture as many of these prey as those spiderlings that made an initial capture. In fact, spiderlings that had already caught a syrphid were more than twice as successful as those attempting to capture a syrphid for the first time [45% (18 of 40) vs. 17% (57 of 330): $G_1 = 14.28$, $P < 0.001$ in a *G*-test of independence]. The syrphid + fruit fly group did not differ in mass from the small group that I provided with several fruit flies after they captured a syrphid ($t_{29} = 0.64$, $P > 0.5$ in a two-tailed *t*-test).

Gains in mass of the syrphid-only spiderlings significantly exceeded those from the field test, those fed on fruit flies only, and those fed with an initial syrphid followed by fruit flies (Fig. 1: $F_{3,20} = 13.66$, $P < 0.001$ in a one-way ANOVA). None of the other groups differed significantly among themselves ($P > 0.05$ in Tukey-Kramer tests). Thus, the laboratory studies using fruit flies presented a realistic estimate of growth in the field.

The spiderlings in the field fed nearly exclusively on dance flies, whose densities varied between 8.0 ± 1.26 and 0.0 flies per goldenrod inflorescence (n = 83–486 inflorescences on

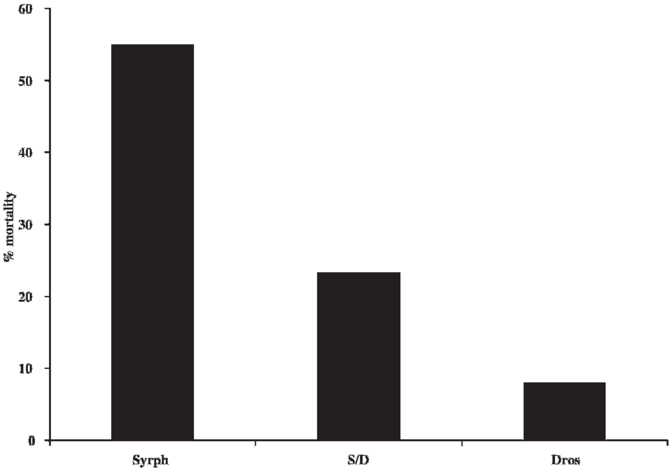

Figure 2.—Percentage of spiderlings that died over one month in growth experiment shown in Figure 1. Spiderling groups as in Figure 1.

different census days from 8–30 clones on evenly-spaced census days over the flowering period), the 0.0 recording a probable consequence of the increasing senescence of these flowers at the end of the season. *Toxomerus marginatus* ranged from 1.1 ± 0.02 to 0.0 per inflorescence in the same censuses. I made no observations of these spiderlings feeding on *T. marginatus* during regular monitoring in the field. Since spiderlings typically feed upon a *T. marginatus* for several hours, my failure to obtain any observations of such a kill during censusing of the spiderlings is consistent with their failure to capture any of them at this time. Given the above-noted infrequent observations of kills made in earlier years, I did not anticipate such an observation during the time devoted to the censuses.

Molt patterns closely followed those of the gains in mass over the study period ($F_{2,61} = 54.02$, $P < 0.001$ in a one-tailed ANOVA). All but one surviving individual fed only on syrphids molted twice during the test period; members of the other groups molted only once, at most. The syrphid-only group averaged 1.9 ± 0.09 molts; the syrphid + fruit fly group, 0.9 ± 0.08 molts; and the fruit fly-only group, 0.8 ± 0.08 molts. The syrphid-only group molted significantly more often than the other two groups ($P < 0.05$ in Tukey-Kramer test); the latter two groups did not differ among themselves ($P > 0.05$: same test).

DISCUSSION

Attacking exceptionally large prey.—Clearly, extreme success in prey capture, such as that attained by some of the syrphid-only spiderlings, can result in large, rapidly developing spiderlings. However, the experiments did not suggest a high probability of such success under field conditions. Individuals capturing a single large prey item appear unlikely to gain significantly more mass or produce more molts over the long term than otherwise similar individuals that fail to make such a capture and otherwise have similar access to prey. Those that captured syrphids in this study did so under considerably more favorable conditions than they would experience in the field and probably approached the maximum rate that a spiderling can hypothetically gain during its early instars. I observed no apparent mortality from this exuberant intake, a source of high mortality among fourth-instar *Nephila clavipes* (Linneaus 1767) reared by Higgins and Rankin (2001). With exception of the few individuals that managed to specialize on *T. marginatus*, the similarity in performance of the spiderlings from the different tests appeared as if constrained by intrinsic factors (Jackson & Rundle 2008). Although capture of a first syrphid enhanced the probability of capturing subsequent ones, a majority of these spiderlings failed to capture a second syrphid, further emphasizing the difficulty of achieving enhanced success in this way. The similarity of gains in mass by the spiderlings fed a single syrphid + fruit flies ad libitum, those fed single fruit flies, and those free-ranging in the field suggests that the group fed single fruit flies served as an adequate control set.

The failure to capture a second syrphid accounted for the high level of mortality through apparent starvation in that group, a result consistent with these individuals subsequently narrowing their range of acceptable prey after an initial experience. These individuals thus serve as a subsequent starvation group. In addition to any effort expended, attacks on extremely large prey often are dangerous (Norris & Johnstone 1998; Roger et al. 2000; Smallegange et al. 2008). Successfully attacked syrphids initially struggled violently for several seconds after spiderlings contacted them and in some instances managed to dislodge the spiderlings by wiping them against the substrate, an action likely to damage the spiderlings' mouthparts and limbs. However, I did not observe these unsuccessful spiderlings continually and thus could not unequivocally establish whether their failure to capture subsequent syrphids resulted solely from refraining to attack them or from the simple failure to make a kill.

Success in the field.—Although sizes of juvenile *M. vatia* in the field vary widely at any given time, this study suggests that the capture of relatively huge prey by second-instar spiderlings does not make an important contribution to this variance. The rather wide range of spiderling emergence dates (Morse 2007) probably plays an important role in the size-spread observed, and differences in initial offspring size (Morse 2000) will further modify the sizes of individuals at a site at any given time. However, low prey availability probably accounts for a strikingly large variation in size and growth rates in the field. Numbers of prey visiting the flowers fluctuate widely, with occasional pulse years and many years in which few are present at the times critical for spiderling growth (Morse 2007). The spiderlings share the ability to engorge themselves with a number of species that depend on highly unpredictable food sources (Schneider & Lubin 1997), though only the pure syrphid diet, unlikely to be achieved in the field, yielded a significantly greater growth rate than that of other ad lib regimes tested.

Since the overwintering mortality of particularly small young may considerably exceed that of individuals completing one or more molts after emergence from their egg sac (Jespersen & Toft 2003; Morse 2007), and size at the end of the season is likely enhanced by high prey numbers, selection should strongly favor the ability to capture profitable prey efficiently. However, the low success rate of concentrating on prey as large as *T. marginatus* seems unlikely to enhance selection for specializing on prey of this size range. Nevertheless, no size groups of *M. vatia* appear to exhibit strong size selection in their attacks on prey (Morse 1979; Erickson & Morse 1997), even though success rates declined with increasing prey size, a common pattern with active prey (Werner & Gilliam 1984; Christensen 1996).

Relation to the life cycle.—As individuals grow, their available resource bases change (Werner and Gilliam 1984). Subsequent juvenile instars enjoy considerably higher success rates in capturing *T. marginatus* than do the second-instar spiderlings. In fact, this abundant prey species is the most important food for many middle-instar *M. vatia* in the study area (Erickson & Morse 1997).

As boom-or-bust hunters adult female *M. vatia* depend on an ability to capture substantial numbers of relatively large prey, but few reach maximum possible size, and most adult females reaching a minimal size for egg-laying (ca 115 mg) will lay their eggs if they do not capture a prey item within a few days (Morse & Fritz 1982; Fritz & Morse 1985). Penultimate female *M. vatia* appear to require unusually large prey items to molt into adults (Morse 1999), a problem seen in other species often lacking sufficient numbers of appropriate-sized prey (Werner & Gilliam 1984; Olson 1996; Persson & Brönmark 2009). These critical demands for large prey by later stages make it plausible that *M. vatia* exhibit a general predisposition to attack prey that are large relative to their own size, even though with experience they might subsequently refrain from such attacks. Such a trait might serve them well at several life stages.

ACKNOWLEDGMENTS

I thank S. Pekar and two anonymous referees for helpful comments on the manuscript. This study was partially supported by the National Science Foundation (IBN98-16692). I thank K.J. Eckelbarger, T.E. Miller, L. Healy, and other staff members of the Darling Marine Center of the University of Maine for facilitating fieldwork on the premises.

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Manuscript received 15 March 2009, revised 7 October 2009.