Oecologia (1997) 109:608–614

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Predator size and the suitability of a common prey

Received: 7 May 1996 / Accepted: 23 September 1996

Abstract Although a predator's mass should influence the suitability of its prey, this subject has received little direct attention. We studied the capture and processing of an abundant syrphid fly *Toxomerus marginatus* (*c.* 4 mg) by 0.6- to 40-mg juvenile crab spiders *Misumena vatia* (Thomisidae) to determine how profitability, relative profitability (profitability/predator mass), overall gain in mass, and relative gain in mass differed with predator mass, and whether foraging changed concurrently. In multi-prey experiments, the smallest successful spiders (0.6–3.0 mg) extracted less mass from flies, and did so more slowly, than large spiders. This gain was proportionately similar to that of 10- to 40-mg spiders with access to many *Toxomerus*. However, many small spiders failed to capture flies. When we gave spiders only a single *Toxomerus*, the smallest ones again extracted mass more slowly than the large ones and increased in mass less than the large ones, but increased in mass proportionately more than large ones. Relative gain in mass from a single prey decreased with increasing spider mass. Spiders larger than 10 mg all extracted similar amounts of mass from a single *Toxomerus* at similar rates, but varied in time spent between captures. Thus, *Toxomerus* changes with spider mass from a large, hard-to-capture bonanza to a small, easy-to-capture item of low per capita value. However, *Toxomerus* is common enough that large spiders can capture it en masse, thereby compensating for its decline in per capita value.

Key words Crab spider · Partial prey consumption · Predator mass · Profitability · Syrphid fly

Introduction

Maximizing gain in energy or mass/handling time (profitability: see Pyke et al. 1977; Pyke 1984) is likely to be a driving force in the lives of many consumers (Schoener 1971), as may relative profitability (profitability/mass of consumer), and measures that incorporate these variables and search time. Prey suitability should thus change over a predator's lifetime as the latter grows, with concurrent changes in hunting, capture, and processing ability. In this paper we evaluate the effect of a predator's mass, a critical, though seldom evaluated, foraging variable, on the profitability and relative profitability of a common prey item, as well as the gain in mass per time and gain in mass per time per predator mass obtained from it when search time is incorporated. Models of foraging (reviewed by Stephens and Krebs 1986) typically focus on differences among the prey available to a predator, thus treating the predator as an implicit constant. Some studies of predator-prey interactions treat performances of predators at different developmental stages, but measure such variables as numbers of prey taken, rather than quantitative gains in mass (e.g., Haynes and Sisojeviç 1966; Hassell et al. 1976), while other studies assess predators' gains in mass quantitatively but do not explicitly investigate predator mass (e.g., Givens 1978; Bailey 1985; Cloarec 1991). However, the mass and trophic appendages of many animals increase several-fold over the parts of their life cycle during which they forage (e.g., Schoener 1967; Fraser 1976), so it is important to evaluate directly their mass as a variable in the context of foraging, profitability, and overall mass gain. Here, we hold prey mass constant and allow predator mass to vary, a seldom-explored approach, which permits us to ask (1) what is the role of predator mass in determining the suitability of a specific prey item?, and (2) do predators change their foraging in response to the suitability of the prey?

Using one important, homogeneous prey species to evaluate the effect of predator mass on profitability and other measures of prey suitability provides insight into the foraging strategy of a predator from a life-history perspective. In some species, tactics may develop that facilitate foraging success at different stages of the life cycle, such as using different prey capture techniques or different hunting locations, as well as different prey (Yo-

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erg 1994). In this paper we evaluate prey capture techniques of different-sized predators of the same species, while holding hunting locations and prey species constant.

The ready availability of an abundant prey species, accessible over much or all of a consumer's life cycle, should prove an important resource to incrementally developing predators. However, if these prey are extremely large relative to early-stage predators, they may prove difficult to capture (Nentwig and Wissel 1986). Also, if a predator eventually grows much larger than a prey species, the profitability of that prey may peak at some point and then decline. Long before this, relative profitability will probably begin to decrease. When the predator reaches a certain mass, it may even prove unproductive to capture that prey: more time and/or energy is expended than reward obtained. Possibly for this very reason, predators that capture their prey one at a time often exclude very small items from their diets (Curio 1976; Morse 1976). Theories of giving-up time (Charnov 1976) and modifications incorporating partial prey consumption (Houston 1990), and profitability (Royama 1970) predict when a prey item should be discarded, but these theories directly address prey variables, not predator variables, as we do here.

Here we investigate the profitability of a single homogeneous prey species to members of a predator species varying over 70-fold in mass. We then calculate relative profitability and subsequently add interprey intervals (search time and resting time) to handling time to obtain a comprehensive view of real intake rates, permitting us to assess the potential importance of a single prey species at different stages of a predator's lifetime. We then ask if these changes are paralleled by changes in the predators' foraging behavior. We evaluate these variables using individuals of the small (*c*. 4 mg) syrphid fly *Toxomerus marginatus* (Syrphidae) as prey for immature crab spiders *Misumena vatia* (Thomisidae) ranging from 0.6 to 40 mg in mass. *Toxomerus* is frequently the most abundant species visiting flowers in its habitat, and at such times is often the most frequent prey species in the diet of *Misumena* ranging over 2.5 orders of magnitude in mass (Morse 1995). Although members of a *Misumena* population cumulatively experience a large number of prey species, prey locally may be dominated by one, or a very few, abundant species (Morse 1995). Further, since a *Misumena* individual may change in mass over its lifetime from about 0.6 mg to as much as 200–400 mg, the number of prey species available to it at any given time may be lower than any list of prey suggests.

Materials and methods

The study area and subjects

We conducted the fieldwork for this study in a 1-ha field in Bremen, Lincoln Co., Maine, and gathered materials for the laboratory studies from this site as well. The field is covered with a variety of grasses, punctuated by several species of forbs, of which goldenrods (*Solidago juncea*, *S. canadensis*, and *S. rugosa*) are the predominant flowering species in late summer, the time of this work. We collected the crab spiders and syrphids used in this study from *S. canadensis*, the commonest of the three species in the study area. These goldenrods bloom sequentially from mid-July to mid-September.

Misumena vatia is a sit-and-wait predator on flowers of fields, pastures, and roadsides. Individuals emerge from their egg sacs in the second instar weighing 0.4–0.7 mg (Morse 1992, 1993). They pass through several instars during which males and females are not externally separable, but in the fourth or fifth (antepenultimate) instar they can be separated by the candy-cane, reddish-brown stripes on the limbs of the males (Gabritschevsky 1927). Both sexes have two anterior pairs of large, raptorial forelimbs, which markedly exceed the posterior two pairs in breadth and length (Gertsch 1939). Spiders used in this study ranged from 0.6 mg (second instar) to 40 mg (female penultimate instars). Female penultimates weigh 20–40 mg or more, and those about to molt into the adult stage usually weigh at least 35 mg (Morse 1995). Adult females can be readily distinguished from the penultimates by a pair of bright, red dorsolateral stripes on the abdomen. Males cease growth at first differentiation and average 3–6 mg. Thus, it is possible that males are represented among the smallest individuals in this sample, but they do not occur among the large ones.

For simplicity we use the terms "large" and "small" to refer to individuals differing markedly in mass, although those terms often refer to body dimensions, rather than mass, in analyses such as this one. Spiders used in this study were all collected from the same substrate, goldenrod at the peak of flowering, and subjected to the same modest regime of starvation, 2–4 days, before testing. Thus, discrepancies in correlations between body dimensions and mass resulting from condition should be minimal (see Nakamura 1972).

Toxomerus marginatus, the prey species used exclusively in this study, is a small, yellow-and-brown-banded syrphid fly that attains extremely high densities on field flowers (Morse 1979, 1981a,b). It reaches its greatest abundance in late summer on goldenrod, when several may occupy an inflorescence simultaneously. Individuals average about 5 mm in length and vary from less than 3 to over 6 mg, averaging about 4 mg, roughly the mass of third- to fourth-instar *Misumena*. Virtually all *Toxomerus* used in this study weighed between 4 and 5 mg. Although much larger than second-instar *Misumena*, these flies sometimes fall prey to them in the field (D. H. Morse, unpublished work). At the opposite extreme, even adult female *Misumena* capture these flies (Morse 1979, 1981a, 1995). Since *Toxomerus* visit most of the flower species in the study area, *Misumena* used in this study have almost certainly experienced them before, with possible exception of the smallest second instars, which have only recently emerged from their natal nests.

Response of young *Misumena* to syrphid flies on goldenrod

For the multiple-prey studies, second through sixth-instar *Misumena*, ranging from 0.6–26.9 mg, were collected from goldenrod and deprived of food for 2–4 days prior to testing. This ensured that they were in a hungry condition and that they hunted actively (Fritz and Morse 1985; D. H. Morse, unpublished work), though they were not grossly starved. Since they capture prey regularly on goldenrod (Morse 1981, 1995), this regime is appropriate, though it does not test for extreme starvation, as in the analysis of Nakamura (1972). Spiders were weighed to the nearest 0.1 mg immediately before testing. A large inflorescence of goldenrod *S. canadensis* was placed in a cage (30×30×30 cm) covered with fine-mesh netting. In order to ensure a visitation rate similar to that in the field, we released 40–50 field-captured syrphid flies into the cage, and placed a spider of known mass onto a branch of the inflorescence. A maximum of four to seven flies occupied the inflorescence at any given time, comparable to the density of individuals on prime inflorescences in the field at times of high *Toxomerus*

density. We noted all prey captures, lengths of times *Misumena* were present on branches of the inflorescence before prey capture, processing times, and total gains in mass for the spiders. Tests were run during the middle of the day, between 1000 hours and 1400 hours, the time of highest fly visitation rates to the goldenrod. Spiders still feeding at 1400 hours were observed until they dropped their prey.

Presentation of single prey

For the single-prey studies, spiders of two size groups were collected (small, 0.6–3.0 mg, and large, 10–40 mg), deprived of food for 2–4 days and then weighed prior to testing. Syrphid flies were captured and weighed to the nearest 0.1 mg in a foil envelope after being chilled in a freezer at –5°C until they became torpid (usually 5–10 min). After recovery, flies were placed into 7-dram vials (5 cm height, 3 cm diameter), one per vial, each occupied by a spider. The spider usually captured the fly, and we noted the time of capture. We randomized flies by mass to ensure that flies available to the two groups did not differ. We made two kinds of feeding measurements:

1. Uninterrupted: we recorded the processing time and the mass (to the nearest 0.1 mg) of both the fly and the spider within 10 min of when the spider dropped a fly.
2. Interrupted: we ran these experiments as in group 1, except that we terminated them after 15 min, 30 min, 1 h, and 2 h (see Pollard 1989), recording the change in mass of both fly and spider at this point. This information permitted us to evaluate the spiders' progress in taking up mass at distinct stages of the feeding period. All measurements of spider and fly mass refer to wet mass.

Prey captured in field

We censused stands of goldenrod in the study area for juvenile spiders with prey items during several days in July and August. We collected and weighed the spiders found with prey, noting time of day and species of prey.

Results

Response to syrphid flies on goldenrod

All spiders captured flies in the goldenrod cage experiments, although probability of capturing prey during an experimental run varied significantly with mass (Table 1). This difference was largely a consequence of the relatively poor success of the smallest spiders (<1.0 mg, second instar), 35% catching flies compared to the average 73% success of all other individuals. Small spiders processed flies for significantly longer than did large ones (Table 2); one 0.6 mg individual actively retained a fly over 829 min (13 h).

None of the small spiders captured more than one fly during a test period (Table 1). In contrast, several of the largest spiders captured and fed on one fly after another, sometimes even holding the first one, feeding on a second, and subsequently returning to the original fly to finish feeding.

Although certain small spiders exhibited a gain in proportional mass that exceeded any others, variance among them was extremely high (Fig. 1). As a whole, prey intake/predator body mass did not differ significantly among the spiders studied (r_s= –0.004, P>0.9, Spearman rank correlation coefficient, Fig. 1). Large spiders retained this parity only by capturing multiple flies (Fig. 1), the number of flies captured increasing with spider mass (r_s=0.941, P<0.002, Spearman rank correlation coefficient, Fig. 2). The large spiders gained significantly more total mass than the small ones in the process (r_s=0.651, P<0.001, Spearman rank correlation coefficient, Fig. 3).

Among spiders obtaining more than one fly, an inverse relationship occurred between mass and the inter-

Table 1 Success of spiders in capturing one or more syrphid flies during 4-h caging experiment: G=10.89, df=4, P<0.05 in G-test

Spider size (mg)	Number that caught prey, with number catching >1 in parentheses	Number that did not catch prey	%Spiders in size range that caught prey
<1.0	6	11	35
1.1–2.0	17	3	85
2.1–3.0	8	8	50
3.1–9.9	13 (2)[a]	4	76
10.0–30.0	13 (9)[b]	3	81
Total	57 (12)	29	66

[a] Number of spiders capturing more than one syrphid in parentheses: both spiders captured two syrphids
[b] Number of spiders capturing more than one syrphid in parentheses: 3 spiders caught 3 flies, 3 spiders caught 4 flies, 2 spiders caught 5 flies, 1 spider caught 9 flies

Table 2 Processing times of syrphid flies (±SD) by different-sized spiders in cages

Mass (mg)	n	Processing time (min)[a]
0.6–3.0	21	339.0±231.4
3.1–9.9	12	144.0±61.5
10–30.0	13	140.2±69.4

[a]Differences among processing times are significant (H=13.32, df=2) in Kruskal-Wallis one-way ANOVA

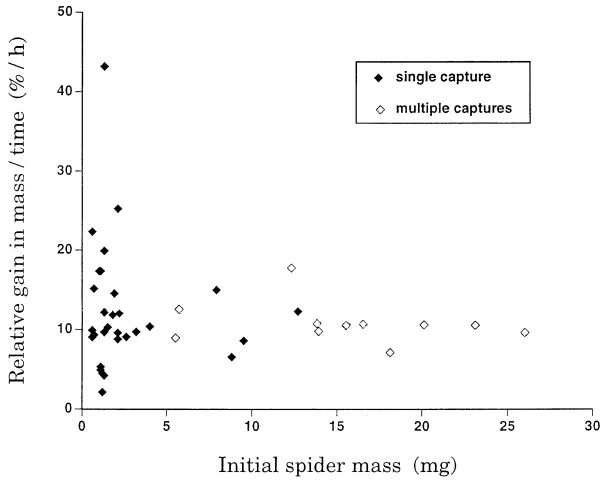

Fig. 1 Relative gain (gain in mass per unit body mass) per hour of different-sized spiders feeding on *Toxomerus*. The caged experimental area permitted the capture of multiple *Toxomerus*

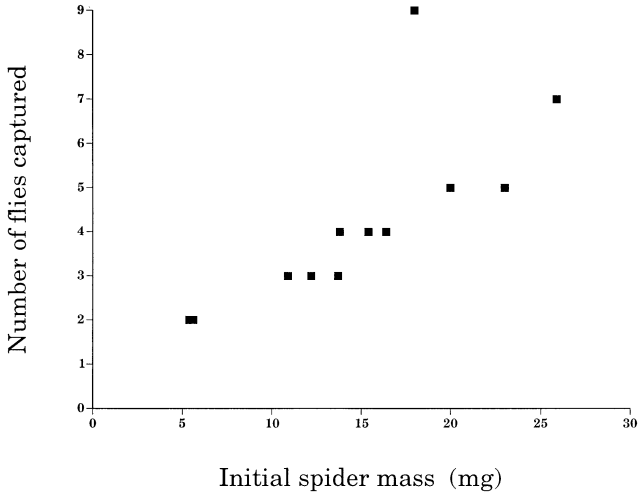

Fig. 2 Relationship between spider mass and number of *Toxomerus* captured over a 4-h period. Only spiders that captured more than one prey are included

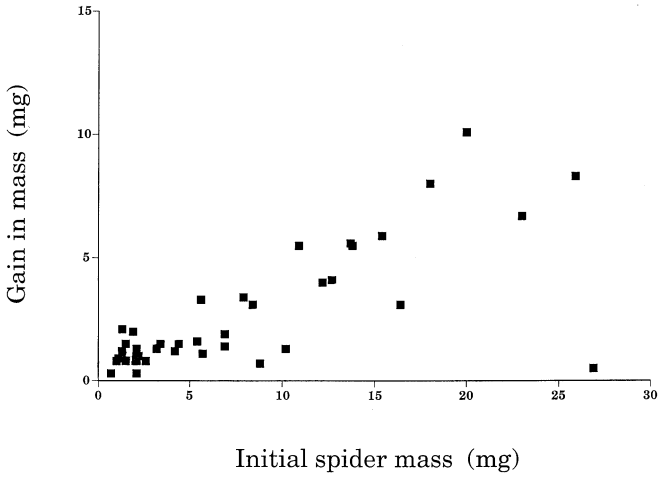

Fig. 3 Gain in spider mass in relation to initial spider mass

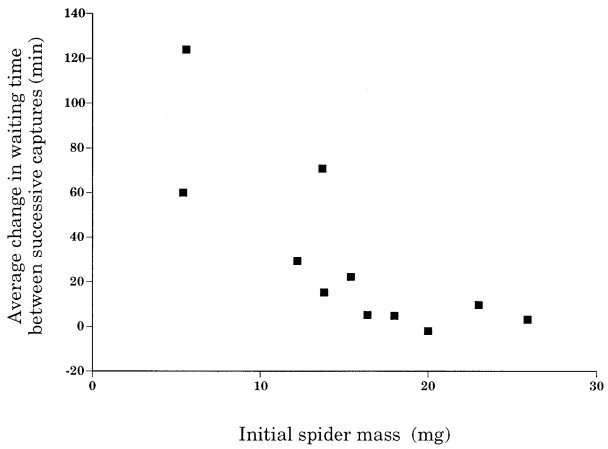

Fig. 4 Change in time between successive captures of *Toxomerus* in relation to spider mass. A time of *0* indicates that successive prey were taken at equal intervals, a *positive* time that the interval between successive captures increased, a *negative* time that the interval between successive captures decreased

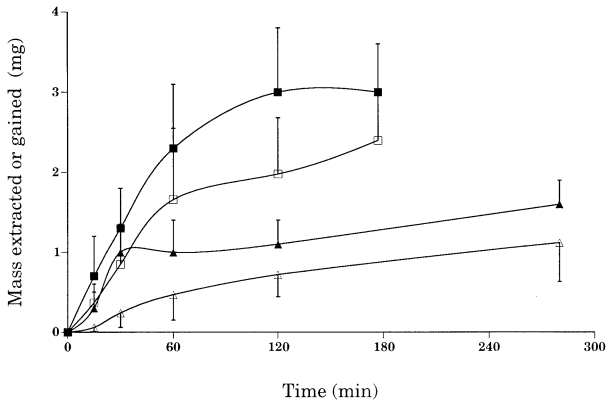

Fig. 5 Mass (±1 SD) extracted from single *Toxomerus* by large (*filled squares*) and small (*filled triangles*) spiders; mass gained from single *Toxomerus* by large (*open squares*) and small (*open triangles*) spiders. Feeding episodes interrupted at periods of 15 to 30, 60 and 120 min, and another group allowed to feed until prey dropped (177 min for large spiders, 280 min for small spiders). To simplify figure, SDs (*bars*) only shown above or below means

val between catches (r_s= –0.873, P<0.01, Spearman rank correlation coefficient, Fig. 4). Additionally, the larger the spider, the more flies it captured (Fig. 2).

Presentation of single prey

The controlled runs with single flies of known mass permitted more precise measures of total gain in mass by the spiders than did the experiments carried out in cages. In captures retained to completion, small spiders gained proportionately more mass on a single fly than large ones (59.8±11.3% vs. 14.4±8.3% gains over previous body mass, U=0, n=25, 26, P<0.001, one-tailed Mann-Whitney U-test), but large spiders registered significantly greater absolute gains in mass than did small ones (2.5±0.6 mg vs. 1.2±0.3 mg gains: U=11, n=26, 25, P=0.001, one-tailed Mann-Whitney U-test). Large spiders also processed these flies for significantly shorter periods than did the small ones (1.8±0.6 vs. 4.8±1.3 h, P<0.001, one-tailed Mann-Whitney U-test).

Spiders over 10 mg all took similar amounts of mass from individual flies, in spite of their four-fold variation in mass (r_s= –0.139, n=26, t=0.688, P>0.2, two-tailed Spearman rank correlation). Thus, though these spiders differed in times between captures with mass (cage experiment), they processed their flies similarly.

In timed runs, large spiders both extracted a significantly greater amount of the initial fly mass, and did so more rapidly than small spiders at each time interval except at 30 min (Mann-Whitney U-tests; Fig. 5).Large individuals extracted more mass from prey in this experiment than from individual prey in the cage experiment (Fig. 3).

All the spiders lost a considerable proportion of the mass they extracted from the flies, though the large spiders both extracted and lost much more total mass than the small ones (Fig. 6). Both large and small spiders ex-

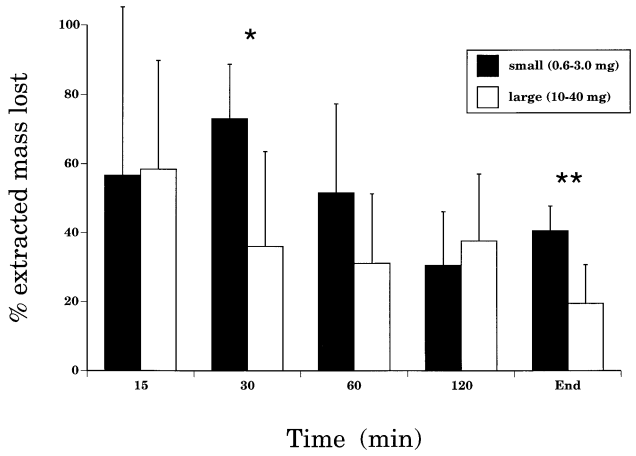

Fig. 6 Percentage of extracted food lost by large and small spiders at different periods during their feeding episodes, (±1 SD). Same data set as Fig. 5. **P*<0.05, ***P*<0.01 in one-tailed Mann-Whitney *U*-tests

Table 3 Mass (±1 SD) of juvenile *Misumena* capturing various prey species

Prey taxon	Number captured	Mass of spider predator (mg)
Toxomerus marginatus[a]	16	11.7±3.9
Larger syrphid flies	5	11.7±4.1
Muscoid flies[a]	24	12.8±5.8
Flies <1 mg[a]	14	5.5±6.3
Wasps[a]	8	21.0±16.5
Thrips	2	2.7±1.3
Moths	3	12.1±4.1
Total, mean	72	11.7±8.5

[a] Original data from these four groups tested by Kruskal-Wallis one-way ANOVA to determine whether the spiders preying on them differed significantly in mass (H=16.77, df=3, P<0.001)

hibited a similar pattern of proportional loss over time, with the exception that large individuals feeding to completion lost proportionately less mass than did small ones (Fig. 6). Initial losses were especially high (Fig. 6) and probably associated with wounds inflicted when the prey was originally killed and from initial feeding efforts. This period of initial loss lasted longer in the small individuals than the large ones and matched the longer overall processing time of *Toxomerus* by the small spiders (Fig. 6).

Profitability and gain in mass

Individual flies were thus more profitable for large spiders than for small, but the reverse held for relative profitability, arguably the more important measure of the two, where predator mass is the variable in question. Incorporating search time and multiple prey, large spiders also exceeded small in gain in mass/time, but relative gain remained similar for large and small spiders as a result of large spiders capturing multiple prey at intervals that decreased with spider mass.

Prey captured in the field

Spiders of the range 0.6–40.0 mg (second through penultimate instars) monitored on goldenrod during July and August 1993 captured 72 insect prey, encompassing a broad range of taxa (Table 3), but dominated by flies (Diptera). *Toxomerus* was the most frequent prey species captured, comprising 20.3% of the total. [Although the spiders captured slightly more muscoids than syrphids (Table 3), these muscoids included several species.] Spiders capturing *Toxomerus* ranged from 5.2 mg to 15.4 mg; thus, none of the smallest category of *Misumena* (0.6–3.0 mg), which made up only 8.9% of this field sample, were observed with them, in spite of their observed ability to capture *Toxomerus* in the trials. Second-instar *Misumena* were observed with both tiny Diptera (Family Empididae) of under 1.0 mg and thrips (Thysanoptera).

Usually these spiders did not appear to discriminate among prey as a consequence of their own (spider) mass (Table 3), although this result may be partly a consequence of the heavy dominance by individuals in the range 5–20 mg (73.4%). One important exception occurred, however: small spiders often captured tiny dipterans (Table 3). Two other possible differences in size preferences involved small spiders capturing the only two thrips prey found and the three largest spiders capturing eumenid wasps (Table 3). None of these spiders captured the largest visitors to goldenrod, bumble bees *Bombus* spp.

Discussion

Our approach to predator-prey interactions is novel, in that we focus on a predatory species' attacks, consumption patterns, and change in mass at different life-cyle stages when exploiting a single abundant, homogeneous prey. Most similar studies have concentrated on other variables such as the importance of different prey species on adult predator diets (Givens 1978), or the functional response of a population to a single prey species (Haynes and Sisojevic 1966). Since flushes of a single prey species may be important even for generalist predators like *Misumena*, our approach addresses a significant event that often occurs under natural situations. Homogeneous prey like adult *Toxomerus* will provide more important rewards for some stages of a predator's life cycle than for others, but with no alternatives, they may be the best foraging option for most *Misumena*. *Misumena* of all sizes attack *Toxomerus* routinely. However, adult females lose mass feeding on *Toxomerus* if they are available for such short periods that only one is captured per day (Morse 1979).

Gains and risks of foraging on *Toxomerus*

Although large individuals in the cage experiment (multiple prey available) extracted food more rapidly than

small ones, their rates of intake per unit body mass did not differ significantly from the small ones. The increased demands of large size were roughly balanced by an increasing frequency of capturing *Toxomerus* as spider mass increased. We have no data on metabolic rate/body mass slopes for *Misumena*, but applying the mean invertebrate slope of 0.75 (Peters 1983; Schmidt-Nielsen 1984) should compensate for any possible slight (nonsignificant) tendency observed for small individuals to gain more mass per unit body mass than large ones (also see Anderson 1970). Any such comparison should also incorporate the low capture rate of the smallest spiders that we tested. Thus, within the range in mass of spiders in this study, the large individuals feeding on *Toxomerus* can maintain a level of exploitation (per unit body mass) equivalent to that of the small ones, as long as they have access to an unrestricted supply of these flies. *Toxomerus* abundance in the field probably often met this criterion on goldenrod during the warm, clear days of late July and August (Morse 1995). However, extrapolating from the success rates of adults on bumble bees (Morse 1979), the larger spiders should be able to improve their rate of input considerably with larger prey. Conversely, *Toxomerus* is an unpredictable resource for the smallest spiders, which are extremely vulnerable to starvation (Vogelei and Greissl 1989; Morse 1993). The poor success of the smallest spiders was clearly a consequence of their limited ability to capture *Toxomerus*, rather than eschewing this species, since they regularly made unsuccessful attacks on *Toxomerus*. In the field, the smallest spiders in fact concentrated on tiny dance flies (Diptera: Empididae) of 0.6–0.9 mg, slightly more than a just-emerged second instar *Misumena* (Morse 1993), although we have several records of second instars capturing *Toxomerus* in the field (D. H. Morse, unpublished work). Often abundant on goldenrod in late summer, and easily captured by second instars (Morse 1993), dance flies thus fill an important role, given the vulnerability of young spiders to starvation (Turnbull 1962; Vogelei and Greissl 1989; Morse 1993). *Toxomerus* clearly provides a bonanza to these small spiders if captured, but is a mainstay for only the somewhat larger spiders.

Some of the spiders that failed to capture prey could have been in a pre-molting condition, during which they are well know to fast (e.g., Haynes and Sisojevic 1966; Foelix 1982). However, the similar collecting and handling regimes used for all individuals should have balanced that factor for the different size groups used.

Although profitability of a prey item is measured by dividing net energy or mass gain by the handling time only (Pyke 1984), intake rates over longer periods must also be discounted by the time individuals must spend searching for their prey, and any decision to hunt for *Toxomerus* should be related to search time as well. Our experiments considered both gain in mass and handling time, but one might argue that they did not adequately consider search time. In this study search time consisted only of the period the spider remained on the goldenrod branch before catching a fly and did not include the time spent seeking a patch. However, since juvenile spiders typically remain on a single goldenrod inflorescence for several days (Morse 1993), *Toxomerus* are abundant under these circumstances, and goldenrods grow in large stands that are not in complete synchrony, patch-seeking probably entails only a small expenditure of time and energy. Thus, the method of accounting used here accurately approximates their time budgets over much of the flowering period.

Both our large and small spiders failed to ingest a sizeable percentage of the prey mass extracted, a probable consequence of evaporative loss (Pollard 1988, 1989). Differences between the two sizes over a feeding episode probably resulted from their respective rates of intake. The larger percent loss of the small spiders at the cessation of feeding may reflect the longer period over which evaporation took place. The losses for both groups at 120 min closely resemble those at which *Diaea* sp. indet., a New Zealand crab spider, discarded slightly smaller *Drosophila immigrans* prey (28%) after 105 min (Pollard 1989). However, large *Misumena* that fed until they discarded their prey lost only 18% of the extracted prey mass, whereas small *Misumena* did more poorly over their much longer handling period, regressing to 38%. Considerable food still remained in the small spiders' prey, but not in those of the large spiders. Most likely, the small spiders became satiated with a single fly, but the large ones did not.

Maximizing gain with *Toxomerus* as prey

It is important to ask whether these spiders maximized their potential rate of prey intake with *Toxomerus*. The inverse relationship of latency between captures and size of 5–15 mg spiders during the cage trials, and the absence of this pattern in 15–30 mg ones, suggest that the smaller individuals came closer to maximizing their possible rate of uptake with *Toxomerus* than did the larger ones (i.e., the small spiders became satiated on *Toxomerus*, but the large ones did not). This conclusion matches the direct relationship between spider size and number of prey captured. The design of the cage experiment did not permit us to measure the mass extracted from each fly of a series taken by a spider. However, the relatively constant mass per fly taken by the spiders weighing over 10 mg in the single-prey experiments is consistent with them spacing intervals between fly captures, rather than strongly altering their intake per fly, to match the level of their hunger.

The similar and short period between captures of the largest spiders we tested also suggests that prey larger than *Toxomerus* would be more profitable for them. Adult female *Misumena* (Morse 1979), the only stage that can capture bumble bees (Morse 1995), achieve a 15-fold or more greater rate of intake from bumble bees than *Toxomerus*, which clearly illustrates this proposed advantage for large individuals. Capturing larger prey

should not benefit the smallest spiders tested, since they did not even remove as much mass from *Toxomerus* as the large spiders, in spite of the extraordinary relative gains attained by some of them.

Toxomerus as a prey item for *Misumena*

Misumena differing in mass by over 1.5 orders of magnitude may thus maintain a positive energy balance from feeding on *Toxomerus*, though these attributes differ markedly with spider mass. However, a decline in *Toxomerus* abundance would likely render it inadequate as a sole prey item for the large spiders before it became inadequate for the smaller ones. Earlier studies with adult female *Misumena* established that these large individuals could not maintain their body mass on *Toxomerus* alone (Morse 1979). Thus, although this study demonstrated a rather similar (flat) proportional gain in mass for spiders of a wide range in mass that had ad lib access to *Toxomerus*, the sensitivity of the conditions surrounding its acceptability as a food item differ markedly. For the smallest, it is a risky bonanza (in terms of starvation probabilities); for the largest juveniles it is satisfactory only if abundant enough to be taken in large numbers.

Acknowledgements We thank S. A. Juliano, C. Harley, J. D. Parrish, S. D. Pollard, D. H. Wise and J. D. Witman for comments on the manuscript and E. B. Noyce for allowing the use of her land. K. S. Erickson was supported by a Howard Hughes Undergraduate Summer Fellowship. Partially supported by the National Science Foundation (IBN93-17652).

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