

The consequences of adult foraging success on the components of lifetime fitness in a semelparous, sit and wait predator

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Summary

We evaluated the role of adult foraging success in the lifetime fitness of female crab spiders *Misumena vatia*. *Misumena* are semelparous, sit and wait predators that hunt for insect prey on flowers, in this study primarily on inflorescences (umbels) of milkweed *Asclepias syriaca*. We used path analysis to integrate previously performed experimental and observational studies, thereby establishing the magnitude, correlations and causal relationships of key foraging and life history variables and their roles in lifetime fitness. A path proceeding from maternal hunting patch choice through maternal mass, clutch mass and number of dispersal-age young was the dominant element and explained a large part of the variation. Other paths that incorporated parasitism of the egg mass and predation of young leaving the nests made only small impacts on variation. No trade-offs were found, primarily because a single factor, maternal mass (a maternal effect) resulting from foraging success, provided major benefits for successive life history stages. Since differences in the numbers of eggs, egg loss and mortality at dispersal resulted almost entirely from differences in maternal mass, they are controlled by the maternal generation and, thus, are appropriately attributed to the lifetime fitnesses of the mothers, rather than to those of their offspring.

Keywords: foraging; life history; lifetime fitness; patch choice; path analysis; spider

Introduction

Selective pressures are ubiquitous forces that may act on organisms at any stage in the life cycle, possibly at more than one place. Their strength, direction and even existence may differ over time or among sites. This being said, very little is known, in the context of entire life cycles, about the factors responsible for differential success in the lifetime fitness attributes of organisms (Arnold and Wade, 1984; Endler, 1986).

Here we investigate certain relationships between life history traits of animals (fecundity, viability, reproductive schedules, etc.) and variables that may ultimately drive the forces of selection acting on these traits. Arguably the most basic of these variables is food acquisition and its vehicle, foraging. If one thinks of life history tactics as ways by which organisms allocate the available resource pool to different parts of the life cycle and foraging tactics as ways by which they set the size of this resource pool (via acquisition), the relationship between these two areas becomes transparent. It then becomes logical to ask how foraging decisions and resulting success influence the basic life history variables of fecundity and survival. The link between foraging behaviour and fitness is a central assumption of optimal foraging theory, yet it has seldom been tested explicitly in the field. Thus, this paper examines how a behavioural trait immersed in a matrix of dependent and independent variables influences these variables and, ultimately, selection. To accomplish this goal we integrate both observational and experimental studies on fitness attributes of foraging patch-choice behaviour by crab spiders *Misumena vatia* (Thomisidae) over their life cycle (Morse and Fritz, 1982; Fritz and Morse, 1985; Morse, 1988a, 1992, 1993a,b) and

the mechanisms associated with them (Morse, 1985, 1987, 1990, 1993c) in the context of lifetime fitness. Experimental manipulations of the critical variables are necessary to establish the causative basis for selection (Grafen, 1988; Wade and Kalisz, 1990), but studies of fitness conducted in the field do not routinely treat this aspect of the question. We use path analysis (Wright, 1968; Li, 1975; Pedhazur, 1982) to evaluate the contributions of differences in adult foraging behaviour and subsequent life cycle events to the lifetime recruitment of offspring (fitness). We include the resulting morphological characters of the animals (expressed as maternal size or clutch size) and their offspring and their interactions with their surrounding environment and other organisms, to identify the major factors that affect juvenile recruitment. The path analysis integrates a large series of studies dealing with the consequences of differential foraging success at different stages of the life cycle (Morse and Fritz, 1982; Fritz and Morse, 1985; Morse, 1988a, 1992, 1993a,b). In this context it can be used to evaluate the relative importance of different causal pathways relating variation in phenotype to variation in fitness (Kingsolver and Schemske, 1991). To the best of our knowledge, these cumulative results provide the first attempt to measure and integrate the lifetime fitness consequences of differences in foraging behaviour that simultaneously incorporates all of the factors likely to modify the results, either directly or indirectly.

We have used *Misumena*, a sit and wait predator on flowers that produces a single clutch of eggs (semelparous), because it offers many advantages for such a study. Most previous studies evaluating behaviour with fitness have used species that reproduce several times (iteroparous), a trait that identifies their biggest operational problem: the resulting wealth of variables (Kamil *et al.*, 1987) may render analysis exceedingly difficult or intractable. *Misumena* thus differs from them in a fundamental way and for this very reason may be an ideal species for initially addressing certain basic questions and problems associated with lifetime reproductive success. It is a relatively common species that can be easily observed and manipulated in the field and female reproductive success is strongly influenced by a small number of hunting events over a short period of time under conditions that can be readily observed and manipulated.

To introduce the stages critical to this analysis we present a synopsis of work directly addressing key aspects of the life cycle. It consists of results from several sets of individuals and thereby differs from a standard analysis in this regard. Arnold (1983) pointed out the virtues of this method for combining studies into wider inquiries that would be infeasible to pursue as single ends in themselves. We ask what aspects of maternal foraging success make the most important contributions to lifetime fitness and what role trade-offs play in this system. We combine these results with those from the experimental papers on different stages of the life cycle in order to present an integrated picture incorporating both the relative importance of the different relationships and the causal relationships among them.

Materials and methods

The organism

The semelparous *M. vatia* has a life cycle of 1 year or more. These spiders frequent flowers that attract large numbers of their insect prey, which consist primarily of bees, flies, moths and butterflies. Typically, adult females lay their single clutch of 75–350 eggs in mid- or late summer. They build their nests on leaves, folding the distal tip under the rest of the leaf and securing it with silk. The eggs are laid in a silken sac between the two resulting thicknesses of the leaf and the leaf is then secured with silk. The female guards the nest from the outside, usually on the underside of the leaf (Morse, 1985), often until the young emerge nearly a month later (Morse, 1987). Young disperse from the nest on foot, on silken lines within the surrounding vegetation or by ballooning (Morse, 1993a) and overwinter as immatures in the litter. Although we suspect that some

individuals overwinter more than once (in early instars the first year and in middle or late instars the second year), at present there is no evidence that they overwinter as adults. Following overwintering, individuals hunt for insect visitors to flowers and males often guard females immediately prior to the latter's moult into the adult stage, when they mate with these females (A. Holdsworth and D.H. Morse, unpublished results). Probably as a result, there are few unmated adult females in the population (Morse, 1988a). Females subsequently grow rapidly if they find hunting sites that attract many large insect prey, sometimes increasing in mass as much as an order of magnitude (40–400 mg or more) within 2–3 weeks. Males are strikingly smaller than females, seldom exceeding 7 mg and averaging 3–5 mg.

Study area and habitats

This work was carried out during the summers of 1979–1992 in Bremen, Lincoln County, Maine, an area of forests and water punctuated by fields and pastures. The study site consisted of a field and adjacent pasture of 1.5 ha, surrounded on three sides by forest and on a fourth by a brushy area. It is described in detail elsewhere (Morse, 1979, 1981a).

These spiders hunt on a wide variety of flowers over their lifespan, but in the study area common milkweed is the species of greatest importance during the immediately pre-reproductive and reproductive stages. Milkweed is a clonal species and in the study area these clones range from 50 to nearly 2500 stems (ramets). Milkweed grows to a height of 80–100 cm in this area and blooms in July, the time at which female *Misumena* are reaching maturity. Milkweed flowers attract by far the greatest concentrations of potential insect prey of any flowers at this time. Flowers are borne on large, round inflorescences (umbels) consisting of 20–70+ flowers, with one to several umbels per stem. The umbels bloom sequentially from the bottom to the top of the stem, such that these discrete patches, typically 2–5 cm apart, often have dissimilar numbers of nectar-producing flowers at any time. Since the numbers of nectar-producing flowers and insects are directly correlated, including those of large insects forming the bulk of adult female *Misumena* prey (Morse, 1981b), these patches vary markedly in their value as hunting sites to the spiders.

Methods

We investigated the stages of *Misumena*'s life cycle potentially critical to lifetime reproductive success between 1979 and 1992, obtaining separate data sets for hunting patch choice (Morse and Fritz, 1982; Morse, 1993c), reproductive success (Fritz and Morse, 1985), nesting success (Morse, 1988a), choice of nest sites (Morse, 1993b), predation on dispersing young (Morse, 1992) and dispersal of young (Morse, 1993a). Additional background and related material on *M. vatia* appear in several other papers, which we will refer to when appropriate. All of these studies include both observational and experimental data. Details on methods are included in the above-cited papers and, consequently, essentials will be presented here only to the extent necessary for discussion.

Misumena's life cycle can be divided into parts directly associated with differential success in prey capture and differential success of offspring. In this study those involving prey capture commenced with the patch choice of maternal foragers hunting at flowers (Table 1) and established the success of individuals hunting at different sites, as measured by subsequent maternal body mass (Fritz and Morse, 1985). The resulting maternal mass can thereby be related to clutch mass (Fritz and Morse, 1985), as well as effectiveness in guarding eggs and emerging young, thereby permitting the identification of both negative correlations (trade-offs) and positive correlations. Possible effects included differential predation on egg masses resulting from maternal guarding before emergence of spiderlings from the nest (Morse, 1988a) and differential predation on emerging spiderlings resulting from maternal guarding (Morse, 1992). The roles of clutch mass, guarding eggs and guarding young were then evaluated in terms of their contributions to the

Table 1. Patch-choice by *Misumena* on milkweed umbels

Variable	Total spiders	% on prime umbel	Reference
Experimentally placed on umbels	42	69.0	Morse and Fritz (1982)
Census of free-ranging spiders	31	71.0	Morse and Fritz (1982)
Experimentally placed on umbels	31	74.2	Morse (1986) ^a
Census of free-ranging spiders	76	80.3	Morse (1988b)
Experimentally placed under plants	34	79.4	Morse (1993c)
Followed over entire period	20	70.0	This study

^a Data presented but not tallied in this study.

$n = 234$, $\bar{x} = 74.0 \pm 4.9$.

number of young available for dispersal (Morse, 1993a). Table 1 itemizes the data sets, sample sizes and references for all of these variables.

We used path analysis in this study to establish the strengths of the causal relationships between the dependent and independent variables. Path analysis includes many aspects of multiple linear regression, but has the added advantage of allowing the construction of putative causal paths with multiple dependent and independent variables. Path coefficients are standardized partial regression coefficients and represent the direct effect of the independent variable on the dependent variable, with all other independent variables held constant.

We constructed the path analysis model to incorporate the major variables in the life cycle and used it, as suggested by Kingsolver and Schemske (1991), to establish the relative importance of different causal pathways relating phenotypic variation to fitness variation. For the path analysis model described in this paper, we used observational data from each of the above-noted studies to evaluate the roles of adult female foraging and intervening factors on lifetime fitness. Based on our earlier studies (citations above), we rejected alternative models that incorporated certain other available variables as unlikely to contribute measurably to the analysis or as biologically unrealistic. The egg number and size (Fritz and Morse, 1985), nest site of parent (Morse, 1993b), hatching success (Fritz and Morse, 1985), destruction of nests (versus the action of parasitoids on broods) (Morse, 1988a), and dispersal of young from nests (Morse, 1993a) play no role or, at most, a minor role, in success as it relates to *Misumena*'s foraging choice, notwithstanding their frequent importance in life history evolution (Cole, 1954; Stearns, 1976). Excluding these factors from the path analysis permitted us to maximize statistical power, which would otherwise be quickly eroded by the presence of several extraneous variables. We emphasize that accurate removal of variables was possible only because we have attained an intimate understanding of the system through many years of in-depth study, including both background natural history and experiments that have focused explicitly on putative causal links of this system (citations above).

Path analyses were performed in SAS using the PROC REG procedure with the STB option on independent variables (SAS Institute Inc., 1985). This procedure generates standardized regression coefficients by dividing a parameter estimate by the ratio of the dependent variable's sample standard deviation to the regression's sample standard deviation. The last section of the path diagram (Fig. 1) requires additional comment. It assesses the relative importance of maternal guarding behaviour before the emergence of young from their nests, clutch size and maternal guarding behaviour after the first emergence on the number of spiderlings surviving until the dispersal stage. However, the data available were atypical in that none of these nests had been parasitized. From other observations we know that when a clutch is parasitized, eggs very seldom

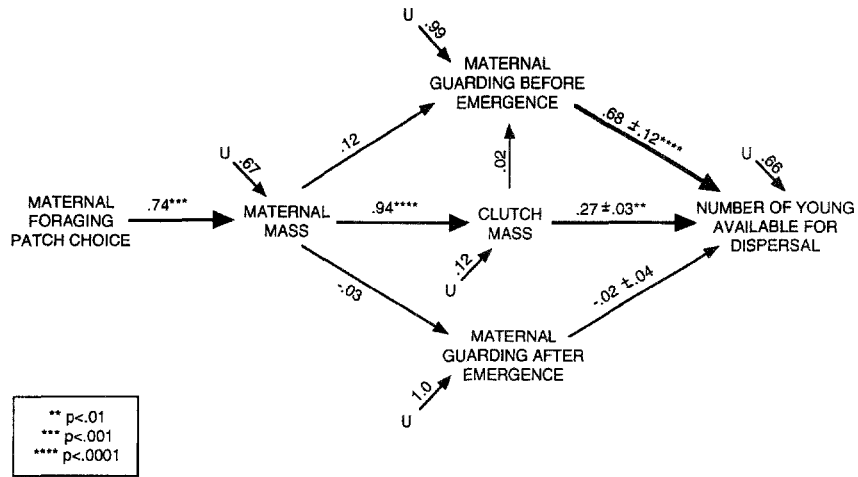


Figure 1. Path diagram of major life history events of female *M. vatia*. Residuals (unmeasured factors affecting dependent variables) are denoted by Us. Path coefficients (standardized partial correlations) are denoted on all other single-headed arrows.

complete development (Morse, 1988a) and, consequently, spiderling dispersal is near zero. Therefore, the impact of parasitism on afflicted broods is catastrophic, but the data necessary to evaluate the importance of parasitism were not available in the results gathered for this purpose.

However, data were available on parasitism rates and the sizes of parasitized clutches in the population at large (Morse, 1988a). This information permitted us to construct artificial data sets that incorporated the role of maternal guarding on spiderling survival in the population at large. Using Monte Carlo methods (Sokal and Rohlf, 1981), we constructed these data sets by randomly sampling from the overall pool of data on these variables accumulated during field observations. These artificial observations were then used, in conjunction with the observations of unparasitized nests, to generate a sample data set with all of the information necessary to evaluate the importance of guarding behaviour before emergence. Incorporation of these simulated data permitted us to assess the relative importance of the three variables in the path diagram (guarding before emergence, clutch size and guarding after emergence) immediately preceding and, presumably directly responsible for, the number of young that dispersed. A sample data set so derived should be treated as a hypothetical result from a pool of possible outcomes. Although one so-derived sample may not be representative of the spider population at large, by generating several such samples we may accurately evaluate the relative importance of this part of the path diagram.

Several assumptions were made in simulating the population of unsuccessful clutches.

(1) Parasitism of brood does not affect subsequent guarding. Since a mother's guarding behaviour remains unchanged whether or not her nest is parasitized (Morse, 1988a), the proportion of unparasitized nests with guarding mothers was set equal to the proportion of derived observations with parasitized nests that had guarding mothers. In this way the proportion of guarded to unguarded nests for both parasitized and unparasitized nests was kept constant without introducing systematic bias, remaining within the bounds of random sampling error.

(2) Clutch size does not affect vulnerability to parasitism. Clutch size for derived observations was randomly selected from within the observed size range of parasitized clutches. Clutch size

itself has no significant impact on the probability of parasitization (variance being primarily due to parental guarding; Morse, 1988a).

(3) Parasitized nests are completely unsuccessful. The number of young available for dispersal was set at zero for each of the parasitized nests constructed, since very few if any spiderlings emerge from parasitized nests (Morse, 1988a).

(4) The derived success rate falls within those found naturally. The nest success rate was taken to fall within the 95% confidence interval of observed success rates in nature.

Path coefficients for the simulated population were calculated in the same way as in the other sections of the path analysis. Since the results are susceptible to extremes because of the randomness that was intentionally introduced into the simulation, 20 data sets were created, using the 20 observations of unparasitized nests and the derived observations of parasitized nests. The path coefficients reported for this simulated part of the analysis are the mean and standard deviation of the 20 path coefficients generated as described here. As such they should be considered as probable path coefficients, with a measure of certainty that is derived from actual observations, as opposed to the directly observed path coefficients reported in other parts of the path analysis.

Synopsis of *Misumena* foraging and life history

We now present basic information necessary for evaluating components of the path analysis. First we consider those variables incorporated into the analysis and then briefly comment on other potentially important variables that did not contribute measurably to variance in earlier studies and thus were not incorporated into the path analysis.

Maternal foraging patch choice

Adult female *Misumena* routinely chose high-quality umbels (Table 1). This result might reflect either the uniform response of individuals choosing high-quality sites most but not all of the time or a mixed population of individuals, some exhibiting perfect or nearly perfect abilities at selecting high-quality umbels and others only making this distinction much less frequently, if at all. Of 20 individuals followed continually over the flowering period of milkweed, 14 chose high-quality umbels each time and six under half of the time (Table 2), closely matching the foraging patterns of both the single-experiment studies and free-ranging individuals in the field (Table 1). Systematic variation in success thus occurred within the members of a population.

Maternal mass

Free-ranging individuals usually varied between 150 and 300 mg at egg laying, with extremes of 114–515 mg (Table 2; Fritz and Morse, 1985; D.H. Morse, unpublished data). Individuals foraging for similar periods on milkweed differed markedly in size at laying as a consequence of their success in choosing high-quality sites (Fritz and Morse, 1985), indicating that these events were of great importance to their reproductive output. Approximately 20% of them even failed to gain enough mass to lay eggs (Fritz and Morse, 1985). Others recruited too late in the flowering period to reach a large size.

Clutch mass

The size of the egg mass was closely and directly correlated with the size of the female (Fritz and Morse, 1985). This relationship ensures that the wide variation in maternal mass before laying is directly transferred onto a later stage of the life cycle.

Maternal guarding before emergence

All egg masses attended by their mothers survived better than did unattended ones, but large egg masses survived through this period significantly more frequently than did small ones. This

Table 2. Summary characteristics of data used in path analysis (all variance expressed as SD)

Character	Data	<i>n</i>	Source of data
Maternal patch choice	High quality 14, low quality 6 ^b	20	This study
Maternal mass (before egg laying) ^a	229.8 ± 56.7 mg		
Maternal guarding before emergence	Parasitized clutches 77, not parasitized 221	298	Morse (1988a), this study
Maternal mass (after egg laying)	76.5 ± 20.8 mg		
Clutch mass	143.4 ± 45.5 mg		
Clutch mass	152.3 ± 44.7 mg	29	Fritz and Morse (1985)
Maternal mass (before egg laying)	231.2 ± 54.4 mg		
Maternal guarding after emergence	Guarded 241, not guarded 210	451	Morse (1992)
Maternal mass (after egg laying)	76.0 ± 17.6 mg		
Young at dispersal	182.6 ± 58.0 per brood	20	Morse (1993a)
Clutch mass	106.1 ± 28.5		
Maternal guarding after emergence	Guarded 13, not guarded 7		

^a This and the following indented characters represent the data used in the part of analysis denoted by unindented characters of the column.

^b High quality, individuals choosing umbels with greatest number of nectar-producing flowers >50% of the time and low quality ≤50%.

advantage resulted from the superior guarding abilities of large mothers (with their large egg masses) – the characteristics of the nests themselves did not contribute to the variance (Morse, 1988a). Thus, the advantage of successful foraging by the mothers before egg laying was transferred onto a subsequent stage and even somewhat enhanced. By far the largest source of mortality resulted from the attacks of an egg predator, the ichneumonid wasp *Trychosis cyperia* (Morse, 1988a).

Maternal guarding after emergence

Predation on emerging young differed significantly at guarded and unguarded nests, but not as a consequence of the earlier foraging success of their mothers, as reflected by either the size of the egg mass or size of the guarding mother (Morse, 1987, 1992). Any mother present easily fended off the primary predator of spiderlings at the nests, middle-instar jumping spiders *Metaphidippus insignis* (Salticidae), which at approximately 5 mg were far smaller than any post-reproductive *Misumena*. Further, although large mothers live longer than small ones (Morse, 1987) and thus should more often be alive and guarding when the young disperse, this potential variable was insufficient to affect the results in this study (Morse, 1992). The advantages of earlier foraging success by large mothers was thus not affected by events during dispersal.

Possible variables not incorporated into the model

We evaluated several other variables for their possible effects on the success of female spiders of different sizes. Three such characteristics (nest site, egg size and dispersal) were rejected as unlikely to play a role in the analysis, but are noted here for the sake of completeness.

Although nest sites of these spiders might differ with body size if different-sized egg masses require different substrates for nest construction or different-sized spiders vary in their mobility and consequent range of sites encountered, neither alternative showed relevant variation (Morse, 1985, 1993b). Eggs varied markedly in size (0.40–0.74 mg), but not with the biomass of clutches (Fritz and Morse, 1985). Spiderlings may disperse from their nest sites by foot, lines in the vegetation or

ballooning, alternatives likely to generate major differences in survival. However, they did not differ in mode of dispersal as a consequence of clutch size, individual size or egg size (Morse, 1993a), eliminating the possibility that size-related dispersal affected success. Substrates initially encountered by emerging spiderlings almost completely dictated whether they dispersed by ballooning or other modes. Since the mode of dispersal was not correlated with the size of eggs or egg masses (Morse, 1993a), subsequent stages of the life cycle should not further modify the differences in reproductive success attained at this point as a consequence of parental success.

Results of path analysis and comparison with experimental results

The path analysis (Fig. 1 and Table 3) illustrates clearly the dominant contribution of the adult females' patch-choice decisions to their success in recruiting young into the pool of dispersers. The patch-choice decisions, which greatly affect the number of prey captured, result in major differences in adult size. Size acts as an inertial force that persists through much of the life cycle, providing large individuals and their offspring with advantages until the young depart from the immediate vicinity of their natal site. Various potential trade-offs (e.g. size of egg mass versus predation in nest or predation on emerging young; Fig. 1) either exhibit positive correlations or no significant correlations occur. In contrast, a trade-off would exhibit a significant negative correlation. If the path between clutch mass and maternal guarding before emergence is removed from Fig. 1, the correlation between maternal mass and maternal guarding before emergence is significantly positive. This result is consistent with our previous experimental analysis of the relationship, which found the former to be non-significant and the latter significant (Morse, 1988a). The correlation between maternal mass and maternal guarding after emergence is near zero, consistent with a non-significant relationship between the two variables in experimental studies (Morse, 1992). Three other potential variables, the relationship between the size of the female and characteristics of the nest site (Morse, 1993b), the size of eggs and size of clutch (Fritz and Morse, 1985) and the size of clutch and predisposition to balloon (Morse, 1993a), showed no nearly significant correlations in the initial experiments and were therefore not incorporated into the

Table 3. Effect coefficients (direct effects plus indirect effects) and proportion of variation explained (r^2) by path coefficient (here denoted as direct effect)

Dependent variable	Independent variable	Direct effect	Indirect effect	Effect coefficient	r^2
Maternal mass	Maternal patch choice	0.74	0.0	0.74	0.54**
Maternal guarding before emergence	Maternal mass	0.12	0.02	0.14	0.02
	Clutch mass	0.02	0.0	0.02	
Clutch mass	Maternal mass	0.94	0.0	0.94	0.88***
Maternal guarding after emergence	Maternal mass	-0.03	0.0	-0.03	< 0.01
Number of young at dispersal	Maternal patch choice	0.0	0.26	0.26	
	Maternal mass	0.0	0.35	0.35	
	Maternal guarding before emergence	0.68 ± 0.04	0.0	0.68 ± 0.04	0.46 ± 0.03**
	Clutch mass	0.27 ± 0.03	0.0	0.27 ± 0.03	0.07 ± 0.01*
	Maternal guarding after emergence	-0.02 ± 0.04	0.0	-0.02 ± 0.04	< 0.01 ± 0.01

*** $p < 0.0001$, ** $p < 0.001$, * $p < 0.01$.

present analysis. Thus, no significantly negative relationships were obtained, either in this path analysis or in the complementary experiments. What the path diagram also makes obvious is that the deviations from the horizontal line directly relating to biomass (guarding before or after emergence of young; Fig. 1) play only a minor role in these interactions. Although the correlation between maternal guarding before emergence and the number of young at dispersal is very high, this correlation represents only a small part of the total variance. Clearly, success in patch choice favours an individual very heavily during subsequent parts of its life cycle.

In general, a large proportion of variation (r^2) in the 'major' dependent variables (maternal mass, clutch mass and number of young) was explained by the path model (Table 3). Among these dependent variables, only the path coefficient between the clutch mass and number of young failed to explain well over half of the variation. In this instance, much of the variation could be explained through indirect effects involving both patch choice and maternal mass, antecedents of clutch mass (Table 3).

Discussion

Trade-offs

Basic life history theory is built on the assumption of trade-offs: gains at one point in the life cycle are secured at the cost of losses at another (e.g. Stearns, 1976, 1992; Sibly and Antonovics, 1992). Only recently has it been generally recognized that trade-offs are not inevitable components of all life history events (e.g. Bell, 1984a,b; van Noordwijk and de Jong, 1986; Scheiner *et al.*, 1989; Arnold, 1992).

Although we identified *a priori* the most likely stages for trade-offs in *Misumena* life history and subjected each to independent bodies of observational and experimental work, we failed to find trade-offs in any instance that we tested. All statistically significant links in the path diagram (Fig. 1), based on the observational data, were positive. Similarly, the experimental data either generated significantly positive correlations between foraging success and success at the subsequent stages tested or the correlations did not differ significantly from zero.

One may further evaluate the significance of the experimental results by summing the number of times that the predicted trade-offs occurred. Five separate stages can be assessed in this way – relating to foraging patch choice (Morse and Fritz, 1982), size of the egg mass (Fritz and Morse, 1985), nest site (Morse, 1993b), mortality of young at emergence (Morse, 1992) and dispersal (Morse, 1993a). The chance probability of obtaining no significant trade-offs is 0.031 (two-tailed binomial test). Thus, the path analysis, generated from the observational data, and the experimental data closely support each other, which greatly strengthens the argument for the dominant causal role of adult foraging in dictating subsequent life cycle success and lifetime fitness as well.

Why, despite the trade-off predictions of life history theory, were no trade-offs observed in this analysis (see Bell, 1984a,b; Scheiner *et al.*, 1989)? If variation in resource acquisition (resulting from foraging success) exceeds variation in allocation of resources to a trait associated with a potential trade-off, then trade-offs may be erased or positive correlations may even appear (Van Noordwijk and de Jong, 1986; Houle, 1991). Positive correlations may occur simply because individuals differ in the total resources that can be devoted to the two traits involved in a potential trade-off. The large variation in foraging success, combined with the high and relatively invariable reproductive effort observed in *Misumena*, would thus account for the absence of trade-offs at this level. The initial advantage of successful foragers generates the size differences that also work to the benefit of these individuals at subsequent stages of the life cycle. Arnold (1992) noted that variation in behaviours promoting the acquisition of resources should be capable of breaking constraints, as was seen in this study. Semelparous individuals should also be expected to allocate

a consistently high proportion of their resources to variables that facilitate reproduction, which would act to minimize variation in allocation.

It may further be important that certain traditional life history trade-offs (e.g. egg size versus clutch size, etc.) did not occur in *Misumena* and that reproductive effort was relatively constant. Those very traits make *Misumena* an especially tractable subject for this type of study, permitting analysis of foraging and life history in the absence of resource allocation as a confounding factor (see Boggs, 1992).

Adult and juvenile contributions to fitness

In addition to the striking differences in reproductive output resulting from previous hunting success, maternal care may play a role at the beginning of the offspring generation. For instance, the success of offspring differed through the nest stage in response to the guarding abilities of mothers, rather than as a direct consequence of the condition of the eggs or nests themselves. This relationship was clearly divulged in a cross-fostering experiment (Morse, 1988a). The extended but variably long maternal contribution enhances the differences in the numbers of offspring in the various broods and, consequently, the variance in parental fitness. Although these aspects of maternal care enhance offspring viability, they are a direct extension of the female's phenotype, not that of the offspring (see Travis, 1988; Kirkpatrick and Lande, 1989). These results thus do not confound a major concern of fitness calculations – that the period of concern combines parts of two generations, thus confounding fitness and inheritance (Arnold and Wade, 1984).

Semelparity and iteroparity

Taken by themselves, these maternal effects should, however, select for retention of resources into the post-reproductive period, thereby lowering reproductive effort (which is very high in comparison with other common sit and wait spiders in the study area: *Xysticus emertoni* (Thomisidae), *Phidippus clarus* and *Metaphidippus insignis* (Salticidae); D.H. Morse, unpublished data). By itself lowered reproductive effort should enhance the opportunity for iteroparity, simply by virtue of the additional resources carried past reproduction. However, we have found no clear evidence of females naturally rearing more than one brood (Morse, 1994) and no sign of adults overwintering in the populations we studied. The short length of the season may contribute to semelparity in our population. Time alone is inadequate for most *Misumena* to rear a second brood in one season, although it is more than adequate for most of them to rear one brood. Situations presenting little chance to reproduce again should favour a high reproductive expenditure (Roff, 1992), potentially leading to semelparity.

The low variance in reproductive effort (Fritz and Morse, 1985) does not suggest the presence of high genetic flexibility for shifts from this semelparous condition. Further, spiders of many species do not overwinter as adults (e.g. Schaefer, 1976; Aitchison, 1984) and this factor alone may drive a population toward producing a single brood, in particular in the case of large spiders, which typically mature later in the season than smaller relatives (Foelix, 1982). However, in spite of the various factors favouring semelparity, one can obtain successful second broods experimentally from members of this population by supplementally feeding females before laying, removing their broods soon after laying and supplementally feeding them again (Morse, 1994). Semelparity thus appears to be environmentally determined in this population and populations in less severe climates may be regularly iteroparous, a pattern found in the green lynx spider *Peucetia viridans* by Fink (1986). The cause and effect relationships between seasonality, semelparity and reproductive effort deserve further attention.

Opportunities for evolutionary change

The failure of one-quarter of the adult females to select optimal foraging sites regularly demonstrates that the population as a whole does not exploit all the potential opportunities for strong fitness pay-offs. The spiders experience some important limitations that may compromise their response to foraging variables. These limitations (a high, constant reproductive effort (Fritz and Morse, 1985), lack of correlation between egg size and clutch size (Fritz and Morse, 1985), inability to overwinter as adults (Gertsch, 1939) and lack of time to produce more than one brood (Morse, 1994)) may have canalized the spiders so that the opportunity for trade-offs is severely limited.

For evolutionary change to occur in response to selection, the relevant traits must have a direct genetic basis. If these traits only vary phenotypically, as in reaching large size under extremely favourable conditions, no evolutionary response can occur. Although tenuous forces such as maternal effects (see Falconer, 1989) may prolong the influence of such phenotypic variation, the absence of differences in *Misumena* offspring relative to clutch size means that advantages to individual offspring will not persist. Heritability of life history traits is lower than that of most other traits (Mousseau and Roff, 1987), although it is believed adequate to provide ample opportunities for selection (Stearns, 1992). However, the ability of these spiders to respond to foraging opportunities may not equal the range of conditions experienced – note that the deficiency in foraging response was obtained repeatedly over many years (Table 2).

Conclusions

Size, resulting from successful patch choice, had both strong direct and indirect effects on subsequent dependent variables that were progressively more directly related to fitness. The initial gain obtained in foraging success created a ripple effect that enhanced success at subsequent stages; therefore, a single advantageous experience may generate the rest. A single event is thus instrumental, rather than one of several acting independently. Grafen (1988) referred to this phenomenon as the 'silver spoon effect' and noted that it may be brought about through a common underlying environmental event during development, a situation akin to the size advantage reported here. Significantly, this fitness advantage persisted and was even enhanced, although it was established nearly a generation before lifetime fitness was to be finally calculated in terms of recruitment of resulting young into the breeding pool. In the process, no trade-offs were experienced that discounted any of these gains. The path analysis closely matched the experimental results obtained from each stage of the study, greatly strengthening the conclusions. Since these young did not differ in size (or presumably in other characteristics) as a consequence of the size of their brood, any advantages to them as individuals resulting from maternal hunting success would disappear upon dispersal, with the sole remaining advantage of maternal success lying in the number of individuals in the dispersing cohort, rather than the attributes of its individuals. This represents the first comprehensive effort to measure and integrate lifetime fitness consequences of differential success in foraging behaviour that simultaneously incorporates all major interacting factors.

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