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Prey availability limits fecundity and influences the movement pattern of female fishing spiders

Received: 13 June 2000 / Accepted: 31 October 2000 / Published online: 28 February 2001
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Abstract We conducted a food supplementation field experiment to test two hypotheses: (1) fecundity of the fishing spider *Dolomedes triton* is limited by a shortage of prey, and (2) the increased movement of adult female *D. triton* exhibited upon maturation is a foraging adaptation to lessen the impact of food limitation on egg production. Free ranging, uniquely marked adult female fishing spiders were assigned either to a food-supplemented group that received crickets in addition to their natural diet, or to a control group. Juvenile female spiders were also marked and their movement patterns were recorded, but juveniles were not offered supplemental food. Food-supplemented adult females gained weight at a faster rate and hatched more than twice as many offspring as control females. Adult females in the control group moved greater distances per day than did juvenile females. Supplemented adult females moved shorter distances per day than control females, and the movement pattern of fed adults did not differ from that of juveniles. These results support the hypotheses that adult female *D. triton* are food limited, and that the increased movement of adult females is a switch in foraging behavior that occurs during the reproductive period. Our finding that natural prey shortages limit egg production contrasts with laboratory-based studies of food limitation in the genus *Dolomedes*, and contradicts a basic assumption of a recent hypothesis that sexual cannibalism in *Dolomedes* is non-adaptive. These discrepancies highlight the importance of insights gained from field experiments with natural populations.

Keywords *Dolomedes triton* · Fishing spider · Food limitation · Foraging mode · Field experiment

Introduction

Food limitation is one of ecology's major themes. The concept is central to theories of how animals forage, how populations grow, and how complex communities are organized. As part of their hypothesis describing the distribution of control processes among trophic levels in terrestrial communities, Hairston et al. (1960) argued that a shortage of prey is a major limiting factor for the predator trophic level in terrestrial habitats. Although their general hypothesis still remains controversial (Strong 1992; Hairston and Hairston 1993, 1997; Polis and Strong 1996), the assumption that prey is often a limited resource for predators might seem less contentious, since many individual predators experience benefits such as increased growth, survivorship, and fecundity when their food supply is increased (see White 1993). Nevertheless, a brief review of the experimental evidence for food limitation in spiders reveals that even for these ubiquitous terrestrial predators, the pattern of evidence is complex (Wise 1993).

Field experiments that supplement prey have demonstrated that some adult female web-building spiders increase fecundity when food is added to the web (e.g., Wise 1975, 1979; Spiller 1984; Ward and Lubin 1993). Likewise, comparisons between field-collected and laboratory-raised wolf spiders have generally indicated that both growth and fecundity of cursorial spiders may also be limited by food in natural populations (e.g., Hagstrum 1970; Kessler 1973; Anderson 1974). However, Greenstone (1978) found no relationship between prey availability and either population density or individual size of *Pardosa ramulosa* (McCook).

Spiders in the genus *Dolomedes* Latreille (Araneae: Pisauridae) are large cursorial spiders associated with freshwater habitats. Spence et al. (1996) failed to find evidence of food limitation when they compared repro-

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duction in field populations of the fishing spider *D. triton* with caged spiders fed on different diets. Similarly, Arnqvist and Henriksson (1997) found no evidence that reproduction is limited by food in a related species, *D. fimbriatus* Clerck. Female spiders maintained in the laboratory on restricted diets did not produce significantly fewer eggs than females maintained on higher amounts.

In contrast, indirect evidence exists that food limitation may affect the foraging behavior of adult female *D. triton*. We discovered that juveniles employ a sit-and-wait strategy, but that females switch to more active foraging upon maturation (Kreiter and Wise 1996). Food limitation and the activity level of individuals are positively related in a number of animal taxa (see Helfman 1990; Werner and Anholt 1993 for reviews). In particular, predatory arthropods are known to switch from a sit-and-wait ambush mode at high prey densities to an active search mode at low prey densities or with increasing food deprivation (e.g., Ford 1978; Griffiths 1980; Johnson and Crowley 1980; Formanowicz 1982; Formanowicz et al. 1982; Inoue and Matsura 1983; Formanowicz and Bradley 1987; Wagner and Wise 1997). In addition to moving greater distances per day, recently matured adult female *D. triton* respond faster and attack distant prey at a higher frequency than even large penultimate juvenile females (Kreiter 1997). These patterns led us to hypothesize that the increased activity of adult female *D. triton* reflects food limitation caused by increased physiological requirements during yolk production (Kreiter and Wise 1996).

Resolution of the question of food limitation in *Dolomedes* may also shed light on another foraging behavior of adult females – sexual cannibalism. Food limitation can increase cannibalism in spiders (Wagner and Wise 1996, 1997) and other predatory arthropods (Polis 1981), and it may play an important role in the specialized case of male cannibalism by females in the context of courtship or mating (e.g., Newman and Elgar 1991; Andrade 1998). Adult *Dolomedes* females are known to cannibalize males (Zimmerman and Spence 1989, 1992; Arnqvist 1992; Arnqvist and Henriksson 1997). Based partly on the lack of evidence for food limitation, Arnqvist and Henriksson (1997) concluded that sexual cannibalism by female *D. fimbriatus* is non-adaptive. Since their conclusion relies heavily on a laboratory-based test of food limitation, it is important to resolve the issue of food limitation in natural populations of *Dolomedes*.

We conducted a field experiment to directly test two hypotheses: (1) reproduction in natural populations of female *D. triton* is limited by prey availability during the adult stage, and (2) the increased activity of adult female *D. triton* is a behavioral response to the increasing energy demands of reproductive activity. In an open, natural population of *D. triton* we supplemented the food of some adult females prior to egg-sac construction, and compared their reproductive measures and movement pattern to control females. We hypothesized that food supplementation would increase fecundity and lead to decreased movement.

Materials and methods

The experiment was conducted on Farm Pond, an artificial freshwater pond in the Patuxent Wildlife Research Center in Laurel, Maryland, USA, that is approximately 60×60 m, with an average depth of 2 m. Principal marginal vegetation consisted of *Eleocharis quadrangulata* (Michx.) Roemer and Schultes, *Juncus effusus* L., *Potamogeton diversifolius* Raf., *Liquidambar styraciflua* L., and *Polygonum hydropiperoides* Michx. The entire margin of the pond was partitioned into 1-m² quadrats by staking with bamboo poles. Maps displaying the features of the pond's perimeter, including vegetation, were used to record locations of *D. triton*.

The margin of Farm Pond was searched for spiders at least four times per week from 28 April to 25 August 1993. Adult female spiders ($n=331$) and juvenile females within two molts of maturity ($n=283$) were captured, measured, and the carapace was marked with Liquitex acrylic paint using the 1–2–4 marking code described by Zimmerman and Spence (1992). Cephalothorax width was measured with calipers and spiders were weighed in the field on an electronic balance. Marked spiders were returned to the same site from which they were taken.

Female juvenile and adult spiders were sequentially given a unique number when first captured. Odd-numbered adult females were assigned to the food-supplementation group ($n=158$), even-numbered adult females to the control group ($n=173$). In addition, some juveniles were assigned to these two groups after reaching adulthood (explained below). The final number of subjects in each experimental group differed because of mortality before the feeding treatment commenced. Spiders in the food-supplemented group were offered one immature house cricket (*Acheta domestica* L.) when returned to the pond after marking and again each time they were re-sighted. Crickets ranged from 1.25 to 2.00 cm in length, weighed approximately 0.05–0.15 g, and were obtained from a commercial source. If a spider refused the cricket, either by ignoring it or by letting it go, the cricket was recaptured. Spiders in the food-supplemented group that were already feeding on wild-caught prey when re-sighted were not disturbed and were allowed to continue feeding without being offered additional food. On average, 2.9 ± 0.1 (SE) days elapsed between sightings; the groups did not differ in frequency of re-sightings [$F_{(1,329)} = 0.25$; $P=0.62$]. The mean (\pm SE) number of crickets accepted by the spiders in the food-supplemented group during the period prior to the construction of the first egg was 2.2 ± 0.1 , ranging from 1 to 7.

Juvenile female spiders ($n=283$) within two molts of maturity were marked and followed for comparison with adult females. Juveniles were not offered additional food items. Molting spiders were re-measured and marked with the same identifying number only if the spider could be identified with certainty. At a minimum, the spider had to be in close proximity to the shed exoskeleton and had to display the characteristic greenish cast of a newly molted individual (Zimmerman and Spence 1992; personal observations). Missing and re-grown appendages were used to assist identification. Seventy-nine juveniles were remarked as adults after molting and were included in the food manipulation component of the study (food supplemented $n=36$, control $n=43$). Adult males were not included in the experiment because their movement patterns more likely reflect a search for mates than foraging for prey.

The average distance moved per day for recaptured spiders was calculated as described in Kreiter and Wise (1996). It was assumed that spiders moved in a straight line from the previous known point, and the distance from that point was divided by the number of days since the last sighting. Each additional sighting resulted in an additional daily mean, calculated for the period between that sighting and the previous sighting. An overall mean of means for each spider was calculated across all intervals, resulting in a single estimate of daily movement rate for each female.

The feeding protocol was continued for each female until an egg sac was constructed. Females were then recaptured, weighed and their egg sacs were marked with unique combinations of colors of acrylic paint. Female *D. triton* grip their egg sacs tightly

in their chelicerae; to minimize disturbance, we weighed females and measured egg-sac diameter while they held their egg sacs. If a female was first observed holding an egg sac more than 1 day since the last sighting, the day of egg-sac construction was interpolated by halving the elapsed time period. The day of egg hatching was also interpolated when necessary.

Like other pisaurid spiders, recently hatched *Dolomedes* spiderlings occur in nursery webs, generally in vegetation near the shore, for approximately 4–8 days after hatching. Nursery webs with hatchlings were collected by cutting the plants containing the webs and placing them in plastic containers. Spiderlings were counted in the laboratory. In contrast to many other pisaurids, females from our population were never seen guarding or associating with the nursery web. Counts of spiderlings were therefore done blindly with respect to the mother's feeding history. After spiderlings had been counted, we identified the mother by the color code on the egg sac. Spiderlings were then released at the pond's margin.

Spiders that were sighted two or more times were used in the analysis of movement. The sampling period for calculating movement of adults was restricted to the time between the adult molt and the construction of the first egg sac. Comparisons of the mean movement per day of juveniles, food-supplemented adult females, and control adult females were made by using a one-way between-groups fixed-effects model ANOVA. We also performed a 2×2 ANOVA to test for a possible interaction between the effects of food limitation (control vs. food supplementation) and net reproductive rate (i.e. whether or not they had constructed at least one egg sac) on the daily distance moved. Multiple comparisons of means were made with Tukey's HSD test.

Several measures of growth and fecundity were strongly correlated with maternal cephalothorax width, as has been reported for other spiders (e.g., Petersen 1950; Turnbull 1962; Wise 1975, 1976, 1979; Enders 1976; Suter 1990; Beck and Conner 1992; Wise and Wagner 1992; Simpson 1995; Arnqvist and Henriksson 1997). Significant Pearson correlation coefficients were found with female cephalothorax width and number of egg sacs ($r=0.26$, $n=321$, $P=0.0001$), diameter of the first egg sac ($r=0.68$, $n=119$, $P=0.0001$), weight gain per day prior to the first egg sac ($r=0.54$, $n=109$, $P=0.0001$), and the number of spiderlings hatching from the first egg sac ($r=0.38$, $n=55$, $P=0.004$) (see Kreiter 1997). Therefore, testing treatment effects on measures with significant Pearson correlation coefficients was done by ANCOVA with female cephalothorax width as the covariate.

Survival was estimated by the number of days that individual spiders were observed. *Dolomedes* are extremely dependent on water, reducing the likelihood that any but the smallest juveniles disperse for any great distances (Carico 1973). We never observed adult females more than 15 cm from the shoreline in over 3 years, and pitfall trapping 1 m from the shore during the summer months never resulted in the capture of even juvenile *D. triton*. Emigration by ballooning from the pond was considered highly unlikely for the older instars, and an adult female's disappearance was presumed to indicate mortality. For spiders that survived to reproduce, the rate of weight gain was calculated as the difference between weight at maturity and the weight of the female with her newly constructed egg sac, divided by the number of intervening days.

Data for all measures are reported as mean \pm SE in the text and figures.

Results

Food limitation of net reproduction

The net reproductive rate of *D. triton* is a function of (1) the proportion of females reproducing, which is determined by the rate of survival to the point at which enough reserves have been accumulated to produce an

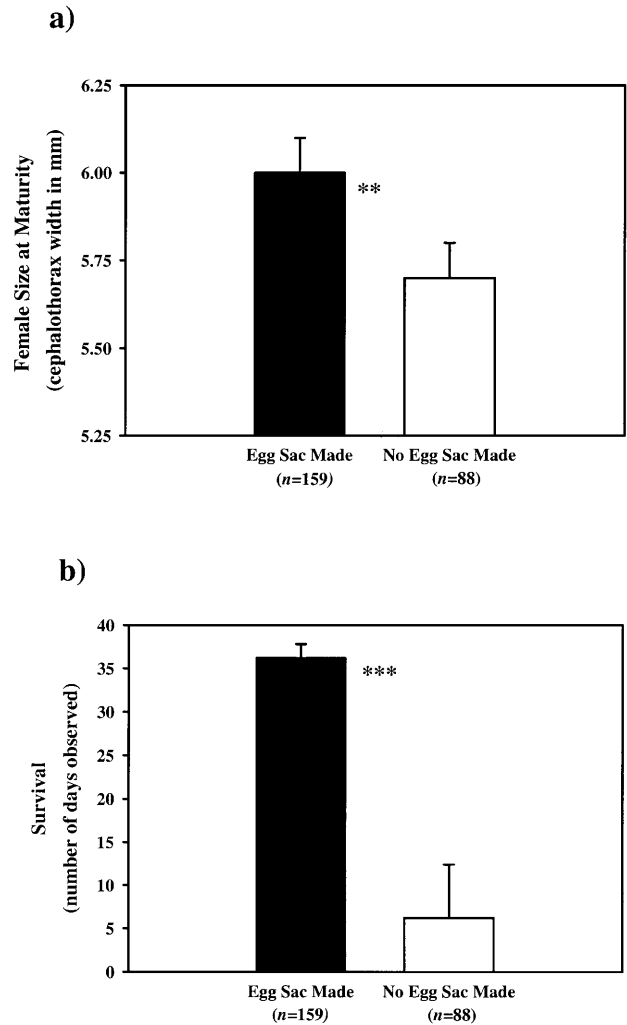
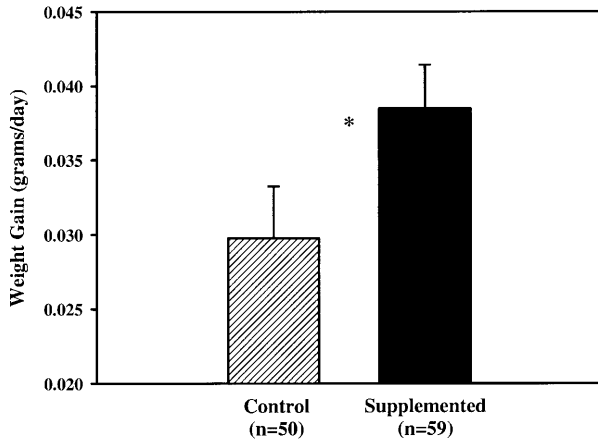


Fig. 1 Relationship between reproductive success of female fishing spiders (one or more egg sacs versus no sacs produced and **a** female fixed size at maturity (cephalothorax width) and **b** survival, measured as number of days observed. Spiders that made at least one egg sac were larger than females that did not make any egg sacs. Spiders that failed to produce an egg sac had a much lower survival rate than females that reproduced. * $P<0.05$, ** $P<0.01$, *** $P<0.001$. Details of statistics in the text

egg sac; and (2) the number of egg-sacs produced and the number of spiderlings that hatch from each sac. The latter parameters are determined by the fixed size at maturity (correlations for *D. triton* presented above) and the rate at which surviving adult females accumulate energy and nutrients for provisioning eggs with yolk.

Although nearly half of the adult female *D. triton* failed to reproduce (43.5% of the 321 marked females disappeared before making an egg sac), supplemental feeding did not increase the likelihood of producing an egg sac nor the total number of egg sacs constructed (Table 1). Supplemented spiders produced 0.79 ± 0.07 egg sacs, while control spiders constructed 0.84 ± 0.06 egg sacs [$F_{(1,318)}=0.89$; $P=0.35$, ANCOVA]. The range for both groups was from 0 to 3. Fixed female size at maturity (cephalothorax width) was an important predictor of

a)



b)

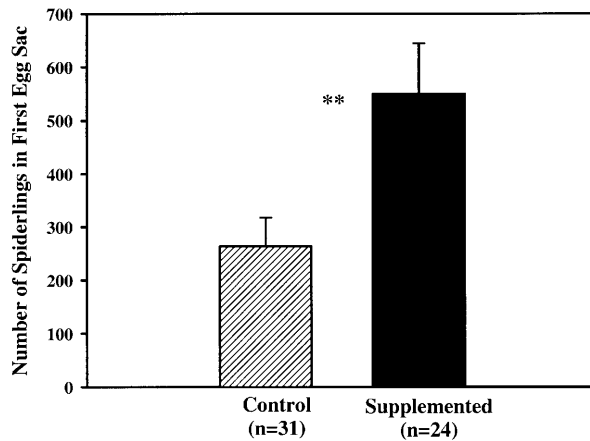


Fig. 2 Effect of food-supplementation on **a** weight gain per day of adult female *Dolomedes triton* and **b** number of spiderlings hatching from the first egg sac. Food-supplemented females gained significantly more weight per day, and produced twice as many eggs per egg sac, than control females. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Details of statistics in the text

reproductive success. Spiders that made at least one egg sac were significantly larger at maturity than females that did not make any egg sacs (Fig. 1a; $t = -2.88$; $df = 245$; $P = 0.004$). Size at maturity was independent of food supplementation in this experiment, because prey were not given to immature spiders.

Rate of female mortality was an important factor determining the proportion of females that reproduced. A 2 (food treatment) \times 2 (reproductive success) factorial ANCOVA revealed that female spiders that never made an egg sac disappeared from the pond much earlier than reproducing spiders [Fig. 1b; $F_{(1,241)} = 162.68$; $P = 0.0001$]. The results gave no indication, however, that a shortage of prey limited survival of adult *D. triton* females. Food-supplemented and control females tended to survive similar numbers of days [24 ± 2 and 23 ± 2 days, respectively; $F_{(1,241)} = 0.78$; $P = 0.38$], and there was no interac-

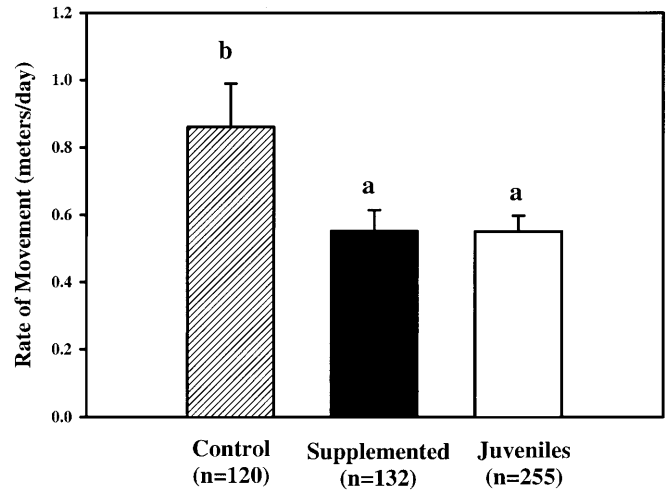


Fig. 3 Effect of supplementing the food supply on average distance moved per day by adult female *D. triton*, with distance moved by non-supplemented juvenile females for comparison. The overall effect of group was significant [$F_{(2,503)} = 4.16$, $P = 0.02$, one-way ANOVA]. Groups with the same letter (a or b) do not differ significantly from each other, while those with different letters differ at the 0.05 level according to Tukey's HSD test

Table 1 Number of egg sacs made by adult female *Dolomedes triton* in the food-supplemented and control groups. There are no significant differences between groups in the mean number of egg sacs constructed. Sampling continued through the end of August, but *D. triton* females have been recorded in Farm Pond with egg sacs until mid-September (personal observation). Therefore, these numbers may slightly underestimate the actual number of spiders that make second and third egg sacs

Egg sacs	Food-supplemented (n=154)	Control (n=167)
0	69 (45%)	70 (42%)
1	58 (38%)	58 (35%)
2	18 (12%)	36 (22%)
3	9 (6%)	3 (2%)

tion between food treatment and reproductive success [$F_{(1,241)} = 0.02$; $P = 0.90$].

Supplementing prey did not significantly alter the number of days required to make the first egg sac [14.0 ± 0.9 and 15.5 ± 0.7 days for supplemented and control, respectively; $F_{(1,56)} = 1.72$, $P = 0.20$, ANCOVA].

In contrast to the absence of an effect of food supplementation on survival and proportion of females reproducing, providing additional prey clearly enhanced the growth rate and fecundity of surviving spiders. The food-supplemented group gained 23% more weight per day than the control group [Fig. 2a; $F_{(1,108)} = 4.15$, $P = 0.04$, ANCOVA], and food-supplemented spiders produced twice as many spiderlings per egg sac as controls [Fig. 2b; $F_{(1,52)} = 8.97$, $P = 0.004$, ANCOVA].

Pattern of movement

Mature females exposed to ambient levels of prey moved 64% farther per day than did juveniles (Fig. 3). Supple-

menting the prey of adult females reduced the distance they moved each day; the resulting rate of movement was identical to that of juveniles (Fig. 3).

Discussion

Reproduction in adult female fishing spiders is substantially limited by a shortage of food supply under normal field conditions. Food supplementation of adult female *D. triton* did not affect survival, but caused them to gain more weight per day and lay egg sacs that hatched more than twice as many spiderlings as the control group. Food supplementation also reduced the movement of adult females to a level equal to that of juveniles. These findings support our hypothesis (Kreiter and Wise 1996) that female fishing spiders increase their foraging movements upon maturation in order to increase the rate of energy acquisition prior to egg production.

Food limitation of net reproductive rate

Our demonstration of food limitation in *D. triton* contrasts with the conclusions of two previous studies of *Dolomedes*. Spence et al. (1996) found no differences in egg numbers produced by free-ranging *D. triton* and those fed *ad libitum* in cages, leading them to conclude that freely foraging adult females were not food limited in either of the 2 years of their study. The mean number of eggs produced in first egg sacs of free-ranging females (approx. 230 ± 21) and high-food caged spiders (approx. 258 ± 33) in their study was almost identical to the number of spiderlings hatching from the first egg sacs of control spiders in our experiment. Our supplementation of prey in the field yielded more than twice as many spiderlings as reported by Spence et al. (1996), even though we counted only hatchling spiderlings and thus probably underestimated the number of eggs produced. Spence et al.'s failure to find evidence of food limitation may be related to undetected effects of caging and/or diet, although it is certainly possible that not all populations of *D. triton* experience food limitation.

Arnqvist and Henriksson (1997) reported that laboratory studies with *D. fimbriatus* failed to demonstrate any effects of adult feeding rate on the number of eggs produced. They argue that female size, determined by juvenile feeding rates, is the major determinant of adult fecundity. Our data corroborate the important role of female size as a predictor of fecundity, but we also clearly demonstrated that under natural conditions, and when female size is statistically controlled, prey availability plays a critical role in the reproductive success of *D. triton*. Even a relatively small amount of supplemental food (2.2 ± 0.1 crickets per female) across the 2-week period of yolk production resulted in a doubling of the number of offspring. The failure of Arnqvist and Henriksson to find a positive effect of food availability on reproduction in *D. fimbriatus* might reflect a differ-

ence in species, or could be related to the design of their study. They report that the number of eggs per egg sac from field-caught spiders did not differ from the combined mean of laboratory spiders maintained under six different feeding regimes. However, sample sizes were small; out of 60 spiders collected for the laboratory rearing, only 14 produced egg sacs. Furthermore, Arnqvist and Henriksson did not report individual means for each of the different feeding treatments, so fecundity in the field cannot be compared directly to fecundity under the lowest and highest rates of feeding in the laboratory. Thus, it remains unknown how natural populations of *D. fimbriatus* might respond to additional food.

We found that a shortage of food strongly limits the number of spiderlings per egg sac by limiting the rate at which adult females add yolk to their eggs. Prey shortages, however, did not affect the days after maturation that elapsed before the first sac was produced. Spence et al. (1996) also found no effect of food level on the time required for *D. triton* to produce an egg sac. These findings contrast with reports from other species (e.g., Austad and Thornhill 1986; Ward and Lubin 1993). Prey shortages were not low enough to affect survival of adult females, even though only about half of them survived long enough to produce an egg sac. The production of an egg sac in our study was positively correlated with size at maturity (cephalothorax width). Smaller females may be less able to survive the adult period than larger females (see also Austad and Thornhill 1986) due to factors such as predation, cannibalism, or disease. Thus, food limitation during the juvenile stage could affect future reproduction because size at maturity is correlated with both the probability of making an egg sac and the number of eggs per sac.

Pattern of movement

While even large juvenile fishing spiders move very little, the final maturational molt is followed by an abrupt increase in movement (Kreiter and Wise 1996). In our field experiment, females that received additional prey failed to show the typical adult pattern of increased activity; instead, their movements were indistinguishable from those of juveniles. This result supports our hypothesis that heightened female activity of adult females reflects a change in foraging behavior associated with food limitation during the adult stage.

The onset of increased movement corresponds to the period when yolk is being accumulated in developing eggs. Yolk accumulation in the eggs of spiders generally occurs in two steps (Seitz 1971; as cited in Foelix 1996): a precopulatory aggregation of fine-grained yolk particles and a second accumulation of larger granules following copulation. The second phase can occur only if enough food is available (Foelix 1996). Thus, increased movement by adult *D. triton*, which disappears when extra prey are provided experimentally, is likely due to an increased need for energy or nutrients above basic metabolic requirements.

This behavioral switch in activity may be comparable to the switch of many invertebrates from a sit-and-wait ambush foraging mode at high prey densities to an active search mode at low prey densities or with increasing food deprivation (e.g., Ford 1978; Griffiths 1980; Johnson and Crowley 1980; Formanowicz 1982; Formanowicz et al. 1982; Inoue and Matsura 1983; Formanowicz and Bradley 1987; Wagner and Wise 1997). Helfman (1990) recognizes the similarity between these situations and optimal diet-selection models that predict a decline in prey selectivity as hunger increases (e.g., Krebs and McCleery 1984). This argument can now be extended to an increased foraging effort in response to reproductive requirements. Provisioning offspring with nutrients is a developmental change that may increase the degree of food limitation experienced by the female. Increased foraging movement offers several potential advantages for a reproductive female, including higher encounter rates with prey (e.g., Huey and Pianka 1981; Richards 1984; Walde and Davies 1984; Grant and Noakes 1987; Skelly and Werner 1990), increased competitive ability (Werner 1991, 1992), and wider dietary breadth (Huey and Pianka 1981; Skutelsky 1995).

Foraging animals adjust activity levels or behavior to reflect predation risks (see Lima and Dill 1990 for a review), and differences in movement between juvenile and adult *D. triton* could reflect different predation pressures based on size differences. However, the switch to increased movement in *D. triton* is neither gradual nor correlated with size, as might be expected if release from predation were solely responsible (Kreiter and Wise 1996). If increasing movement is not related to size and actually results in a higher food intake for adult females, then juveniles might also benefit from an active strategy as well. Increased prey consumption as a juvenile should result in a larger, more fecund adult. However, juveniles in our studies typically employ a sit-and-wait foraging style. This apparent discrepancy underscores the need for a better comparative understanding of juvenile and adult dynamics. Active movement may be more dangerous for juvenile *D. triton* in terms of predatory risk and cannibalism. The sedentary behavior of juveniles may reflect a trade-off between the increased risks and long-term benefits of movement (e.g., Sih 1987; Lima and Dill 1990; Werner and Anholt 1993). On the other hand, the energetic requirements of yolk production may place different, more immediate, temporal constraints on adult foraging compared with juveniles.

Food limitation and sexual cannibalism

Several hypotheses have been proposed regarding the selective benefits of sexual cannibalism in spiders (see Elgar 1992; Johns and Maxwell 1997 for reviews of the hypotheses). Acquisition of extra food is an hypothesized benefit of sexual cannibalism for females (e.g., Matsuro and Morooka 1983; Liske and Davis 1984, 1987; Birkhead et al. 1988; Newman and Elgar 1991),

leading to the prediction that cannibalism should be more likely if the female is hungry, despite the cost of losing a mating. Arnqvist and Henriksson (1997) tested this prediction for the fishing spider *D. fimbriatus* in a laboratory setting. They found no effect of food consumption on either egg production or aggression towards males. The authors proposed a non-adaptive model of the evolution of sexual cannibalism in *D. fimbriatus*, based on selection for indiscriminate aggression in juvenile instars. They conclude that sexual cannibalism by adult female fishing spiders is non-adaptive because it incurs considerable cost in terms of lost insemination opportunities, yet confers no advantage because rate of prey intake by mature females does not limit egg production. However, it is difficult to assess from their laboratory study the actual degree of food limitation of female *D. fimbriatus* in nature. Our direct demonstration of severe food limitation in a natural population of a related *Dolomedes* species suggests a selective benefit for the cannibalistic behavior of female fishing spiders – that of increased offspring. Selection for aggression in females during the adult period based on alleviation of food limitation is an alternative to selection for aggression in juveniles as an explanation of the observation that virgin female *Dolomedes* will cannibalize potential mates.

In conclusion, our field experiment demonstrated that reproduction in adult female fishing spiders is food-limited in a natural population. Supplementing the diet with additional prey resulted in greater weight gains and more offspring than at ambient levels of prey capture. Increased activity is typically associated with maturation in *D. triton*; the provision of additional prey for adult females changed their movement pattern to one indistinguishable from that of juveniles, suggesting that adult females respond to the effects of food limitation during yolk formation with increased foraging effort. Our finding that reproductive success in female *D. triton* is food-limited contrasts with previous studies of *Dolomedes* spp. Our demonstration of strong food limitation fails to support the basic assumption of a recently proposed hypothesis that sexual cannibalism in fishing spiders is nonadaptive. This contrast in findings illustrates the value of field experimentation with open, natural populations in tests of evolutionary hypotheses dependent on ecological assumptions.

Acknowledgements We thank the Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, for providing our research sites. We are indebted for their continued support of this research. James Wagner joined in valuable discussions during the experimental planning and David Clissold, Dan Formanowicz, David Reznick, and two anonymous reviewers provided helpful comments on the manuscript. This research was supported in part by a Special Research Initiative Support award from the University of Maryland Graduate School, Baltimore.

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