1994. The Journal of Arachnology 22:185–189

EFFECTS OF FISH ON THE GROWTH AND SURVIVAL OF TWO FISHING SPIDER POPULATIONS (*DOLOMEDES TRITON*; ARANEAE, PISAURIDAE)

Chester R. Figiel, Jr. and **Gary L. Miller**: Department of Biology, University of Mississippi, University, Mississippi 38677 USA

ABSTRACT. Our objectives were to determine if *Dolomedes triton* from two populations, one with fish predators and one without, differed in growth and survival. Using a 2 × 2 randomized block design, equal numbers of spiders were reared over a six-week period in artificial pools in the presence and absence of a natural predator, the bluegill sunfish, *Lepomis macrochirus*, (Perciformes: Centrarchidae). Neither spider body size nor spider survival differed between populations. Survival of spiders in pools with fish was not significantly different from spiders in fishless pools. However, spider body size was significantly smaller in pools containing fish compared to spiders in pools without fish. No significant interaction between population source and the presence of fish was detected. We suggest two mechanisms for the reduction in spider body size: interference (i. e., avoidance of fish) and exploitative competition with fish for food resources. The reduction in spider body size is important because of the relationship between spider size and reproductive success (larger females may produce a greater number of offspring than smaller females; larger males may copulate with more females than smaller males). Because these spiders are found in wetlands areas where sunfish occur, our results suggest that these spiders may adjust to competitor/predator-rich environments through compromises in growth and development.

Predators can directly influence the structure and dynamics of aquatic communities by differential predation on species (Wilbur 1980). Indirectly, predator presence can influence prey by altering prey morphology, life history, or behavior (reviewed in Kerfoot & Sih 1987; Lima & Dill 1990). For example, prey behavioral patterns may change in response to predator presence and subsequently affect competitive or foraging tactics of the prey (Morin 1983; Werner et al. 1983; Power et al. 1985; Gilliam et al. 1989). These behavioral modifications can change with respect to ontogenetic development if the predator-prey relationship is based on body size differences (see Werner & Gilliam 1984). Thus a predator-prey relationship early in prey development may be altered to a competitive relationship through time. Understanding the effects of competitors and predators on the behavior of interacting species can identify the mechanisms of selection that are responsible for differences within populations in life history traits (e. g., growth, reproductive success).

In many species of spiders, growth and body size are directly related to reproductive potential (e. g., number of eggs produced) and mating success (Fritz & Morse 1985; Smith 1990; Brady 1993), and are also indirectly related to survival (Rayor & Uetz 1990). In addition, smaller spiders may be more vulnerable to predatory encounters with conspecifics (Bleckmann & Barth 1984). Predators may modify these life history traits by influencing spider activity, exploiting food resources or by altering spider habitat use (van Berkum 1982; Rayor & Uetz 1990; Riechert & Hedrick 1990). Van Berkum (1982) hypothesized that *Trechalea magnifica* spiders may forage nocturnally to avoid predation risk during the day, in spite of the greater prey abundance available during the day. Riechert & Hedrick (1990) examined predator assessment of two populations of *Agelenopsis aperta* spiders and determined that the population exposed to predation pressure exhibited a longer latency period to return to a foraging mode following a predatory encounter. Few studies, however, have measured directly the effects of predator presence on spider foraging activity or feeding rates in terms of growth, body size, mating, or reproduction – traits that are closely related to fitness (but see Rayor & Uetz 1990).

The objectives of this study were two-fold: 1) to examine the effects of fish presence on the growth and survival of the fishing spider, *Dolomedes triton* (Walckenaer), and 2) to test for differences in growth and survival between two populations of spiders: one population from ponds containing fish, and one population from locations that lacked fish.

EXPERIMENTAL SYSTEM

Dolomedes triton is a widely distributed species in the United States and Canada, foraging on or near the surface of ponds or slack water areas of streams and rivers, and use the water's surface to capture prey or escape predation (Carico 1973). Attack behavior by these spiders can be elicited by water surface waves generated by prey (Bleckmann & Barth 1984; Bleckmann 1985; Bleckmann & Lotz 1987). The sensory ecology of *D. triton* spiders, with regards to foraging has been examined (Bleckmann & Barth 1984; Bleckmann & Rovner 1984; Bleckmann 1985), as has their courtship behavior (Roland & Rovner 1983; Bleckmann & Bender 1987), and prey use (Zimmermann & Spence 1989).

The bluegill sunfish, *Lepomis macrochirus*, is syntopic with *D. triton* over most of its range. These sunfish have a diverse diet and will eat a wide variety of arthropods including *D. triton* (CRF pers. obs.). These sunfish and *D. triton* often occupy the same microhabitats of ponds (e. g., shallow shoreline areas) because of interactions with larger predatory fish (Werner et al. 1983; CRF pers. obs.).

METHODS

We measured growth and survival of *D. triton* collected from two populations: Savannah River Plant, Aiken County, South Carolina (SC) and the University of Mississippi Biological Field Station, Lafayette County, Mississippi (MS). Spiders were collected from two SC ponds on 31 July 1992 and from three MS ponds on 3 August 1992 to ensure local population replication. We chose these two populations to ensure that gene flow between the populations was low or nonexistent. Additionally, we chose SC ponds because they have lacked fish for at least 20 years, (J. Pechmann pers. comm.), while the MS ponds have had fish present for the last 40 years, *L. macrochirus*, *Pimephales promelas* (flathead minnows) and *Micropterus salmoides* (largemouth bass) (B. Knight pers. comm.).

Spiders (X carapace length at the start of the experiment ± SD: $X_{SC} = 3.5$ mm ± 0.1 mm, $X_{MS} = 3.5$ mm ± 0.2 mm) were reared in the presence and absence of *L. macrochirus* in artificial ponds (plastic wading pools, 1.52 m diameter, 22 cm deep). We used a 2 × 2 factorial experiment to examine the main effects and interactions between fish presence and population source. We randomly assigned the four treatment combinations within each of four replicate blocks for a total of 16 pools. Pools [within size ranges of natural ponds inhabited by these spiders (CRF pers. obs.)], were placed in an outdoor fenced enclosure on the Edward J. Meeman Biological Station (EJMBS) in Shelby Co., Tennessee, which exposed them to natural photoperiod, seasonal rainfall and temperature. Pools were filled with tap water on 22 July 1992 and window screening was placed over pools to prevent frogs and insects from colonizing them and prevent spiders from escaping. We added logs, detritus, floating sponges, and leaf litter to pools to provide habitat complexity, refuge, and substrates for spiders.

We seined *L. macrochirus* ($X = 43$ mm total length ± 2.4 mm SD) from a pond located on the EJMBS to serve as our model predator. Bluegill sunfish this size can vigorously attack, injure, and consume *D. triton* (CRF pers. obs.). Two fish were used per pool (0.8 fish per m^2 of pool surface area; within range of densities of fish in natural ponds, Hall & Werner 1977). Likewise, the treatment level of *D. triton* (four spiders per pool) is within the range of spider densities in natural ponds in Mississippi (1.6 spiders per m^2, CRF unpubl. data). Spiders and fish were placed in pools on 17 August 1992. *Hyla chrysoschelis* tadpoles were used as prey for spiders and fish and were collected from nearby ponds. We supplemented prey in pools by adding crickets (*Achetus* spp.) from a commercial colony. Either five similar-sized crickets or five similar-sized tadpoles were added to all pools once every five days. Spiders readily capture and consume these prey in the lab. The experiment was terminated on 28 September 1992 and all spiders and fish were preserved in alcohol.

Spider body size was determined by measuring the carapace length on preserved specimens. Response variables in the experimental treatments were mean growth (increase in length of carapace, measured to the nearest 0.5 mm) and survival (the number of surviving spiders divided by initial number) for each pool. Proportions of surviving individuals from the initial number were arcsine transformed, and body size data were log transformed before analyses.

RESULTS

Survival was not correlated with body size at the end of the experiment ($r = -0.224$), thus

Table 1.—Summary of the two-way analysis of variance on body size (carapace length) and survival of *Dolomedes triton* from two populations reared in the presence and absence of fish, *Lepomis macrochirus*. Body size data were log transformed and percent survival data were arcsine square-root transformed before analysis.

Source of variation	*df*	*MS*	Test of significance
Body size			
Population	1	0.00011	$F = 0.165$ $P = 0.6957$
Fish presence	1	0.00948	$F = 14.856$ $P = 0.0023$
Population by fish	1	0.00001	$F = 0.017$ $P = 0.9008$
Error	12	0.00064	
Total	15		
Survival			
Population	1	0.00428	$F = 0.086$ $P = 0.7778$
Fish presence	1	0.03855	$F = 0.771$ $P = 0.4062$
Population by fish	1	0.10709	$F = 2.143$ $P = 0.1689$
Error	12	0.04998	
Total	15		

growth data were analyzed independently of survival data. Analysis showed there was no block effect and data from the four blocks were subsequently pooled for analysis.

Body size of spiders was affected by the presence of fish (Table 1). At the end of the experiment, spider body size was significantly smaller in pools containing fish (X_{SC} = 4.85 mm ±0.21 mm; X_{MS} = 4.93 mm ±0.17 mm) compared to body size of spiders in pools without fish (X_{SC} = 5.45 mm ± 0.34 mm; X_{MS} = 5.50 mm ±0.45 mm). Body size did not differ between the SC population (5.15 mm ±0.41 mm) and the MS population (5.21 mm ±0.44 mm) at the termination of the experiment (Table 1). No significant interaction between population source and the presence of fish was detected (Table 1).

Spider survival did not differ between populations (Table 1). At the end of the six-week experiment, the percent survival of spiders from SC was 50.0% ±23% and from MS 46.9% ±22%. Survival of spiders in pools with fish (X_{SC} = 62.5% ±25%; X_{MS} = 43.8% ±14%) was not significantly different compared to survival of spiders in fishless pools (X_{SC} = 37.5% ±14%; X_{MS} = 50% ±29%) (Table 1). No significant interaction between population source and the presence of fish was detected (Table 1).

DISCUSSION

Body size of spiders differed significantly after just 42 days and clearly indicates that fish presence influenced spider growth. Two mechanisms could be responsible for these results: interference (i. e., spider avoidance of fish) or exploitative competition with fish for food resources. Behavioral observations of *D. triton* placed with *L. macrochirus* in laboratory aquaria determined that these spiders avoided bluegill sunfish by altering location in aquaria (CRF unpubl. data). If this behavior influenced *D. triton* foraging time or effort, as has been shown for other spiders (van Berkum 1982; Riechert & Hedrick (1990), this could account for the reduction in *D. triton* body size.

Additionally, competition for prey between sunfish and spiders probably resulted in a reduced food resource base for spiders, and subsequently resulted in a reduced spider body size. Although we did not directly measure food resource levels in pools, sunfish can prey on tadpoles and floating crickets, and food resource level can be decreased in these pools due to fish presence (Figiel & Semlitsch 1990). Periodic searches for prey determined that no prey survived in pools containing sunfish, whereas these prey were available and abundant for spiders in pools without fish. This suggests that the reduction in spider body size probably resulted from exploitative competition between fish and spiders, with the additional pressure of predator avoidance. Because food resource levels for spiders in fishless pools were abundant, differences in spider body size in natural conditions may occur only when prey densities for spiders are relatively high or fish densities are low.

It is difficult to determine reasons for the lack of differences between populations in growth or survival, or in lack of differences in survival between fish and fishless ponds, particularly considering that the SC populations have lacked fish in these ponds. With respect to survival, it is possible that mortality related to the experimental situation is high thereby masking effects of the predator. A shorter experiment using larger ponds might alleviate this problem if it exists.

However, there may be a biological basis for the lack of differences in growth and survival in fish and fishless ponds. Conceivably, lack of interpopulational variation in growth or survival resulted from selection for phenotypic plasticity in these life history traits. This may be an effective way for spiders to adapt to highly variable environments rather than favoring specific phenotypes (Caswell 1983; Kaplan & Cooper 1984; Petranka & Sih 1987). Potentially, the relatively short period (at least 20 years) SC spiders have been in ponds without fish may not be long enough for selection to influenced the behavior of these spiders. Additionally, there is an abundance of underwater competitors and predators other than fish (e. g., dragonfly larvae, salamander larvae, dytiscid beetles) that are temporally or spatially present that could influence spider behavior, growth, development, or survival. The diversity of potential predators/competitors could select for the observed plasticity. Further, the interaction between fish and spiders may change over time from a predator–prey relationship to a competitive relationship when spiders reach a larger body size (and potentially into a spider predator–fish prey interaction).

The importance of body size reduction in *D. triton* is observed in the relationship between body size and reproductive success: in many species, larger females may produce a greater number of offspring, and larger males may copulate with more females that smaller males (Fritz & Morse 1985; Smith 1990; Brady 1993). Large body size also confers an advantage to individuals in escaping gape- or size-limited predators; thus smaller spiders may be more vulnerable to predatory encounters (Bleckmann & Barth 1984). Because these spiders are found in wetlands areas where sunfish predators occur (Carico 1973; CRF pers. obs.), our results suggest that spiders may adjust to habitats containing fish through compromises in growth and development. Further studies examining *D. triton* habitat use and behavior, and the interactions and trade-offs involved in foraging in predator/competitor-rich environments are needed.

ACKNOWLEDGMENTS

We thank B. Houston, K. Kallies, D. Reimers, P. Smiley, and A. Williams for their help in collecting spiders. We thank G. Wein for access to ponds in South Carolina and M. Kennedy and the Edward J. Meeman Biological Station for the use of facilities. We appreciate the comments and criticisms on earlier versions on this manuscript from H. Farris, R. Holberton, and G. Stratton.

LITERATURE CITED

Bleckmann, H. 1985. Discrimination between prey and non-prey wave signals in the fishing spider *Dolomedes triton* (Pisauridae), Pp. 215–222, *In* Acoustic and vibrational communication in insects (K. Kalmring & N. Elsner, eds.), Parey Verlag, Berlin.

Bleckmann, H. & F. G. Barth. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behavior by surface waves. Behav. Ecol. Sociobiol. 14:303–312.

Bleckmann, H. & M. Bender. 1987. Water surface waves generated by the male pisaurid spider *Dolomedes triton* (Walckenaer) during courtship behavior. J. Arachnol., 15:363–369.

Bleckmann, H. & T. Lotz. 1987. The vertebrate-catching behaviour of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). Anim. Behav., 35:641–651.

Bleckmann, H. & J. S. Rovner. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). I. Roles of vegetation and wind-generated waves in site selection. Behav. Ecol. Sociobiol., 14:297–301.

Brady, R. A. 1993. The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). J. Arachnol., 21:91–106.

Carico, J. E. 1973. The Nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). Bull. Mus. Comp. Zool., 144:435–488.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. American Zool., 23:35–46.

Figiel, Jr., C. R. & R. D. Semlitsch. 1990. Population variation in survival and metamorphosis of larval salamanders (*Ambystoma maculatum*) in the presence and absence of fish predation. Copeia, 1990: 818–826.

Fritz, R. S. & D. H. Morse. 1985. Reproductive success, growth rate and foraging decisions of the crab spider *Misumena vatia*. Oecologia, 65:194–200.

Gilliam, J. F., D. F. Fraser & A. M. Sabat. 1989. Strong effects of foraging minnows on a stream invertebrate community. Ecology, 70:445–452.

Hall, D. J. & E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. Trans. American Fish. Soc., 106: 545–555.

Kaplan, R. H. & W. S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin-flipping" principle. American Nat., 123:393–410.

Kerfoot, W. C. & A. Sih. 1987. Predation: Direct and Indirect Impacts on Aquatic Communities. Univ. Press of New England, Hanover, New Hampshire.

Lima, S. L. & L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian J. Zool., 68:619–640.

Morin, P. 1983. Predation, competition, and the composition of larval anuran guilds. Ecol. Monogr., 53:119–138.

Petranka, J. W. & A. Sih. 1987. Habitat duration, length of larval period, and the evolution of a complex life cycle of a salamander, *Ambystoma texanum*. Evolution, 41:1347–1356.

Power, M. E., W. J. Matthews & A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology, 66:1448–1456.

Rayor, L. S. & G. W. Uetz. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. Behav. Ecol. Sociobiol., 27: 77–85.

Riechert, S. E. & A. V. Hedrick. 1990. Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta*. Anim. Behav., 40:679–687.

Roland, C. & J. S. Rovner. 1983. Chemical and vibratory communication in the aquatic pisaurid spider *Dolomedes triton* (Araneae: Pisauridae). J. Arachnol., 11:77–85.

Smith, G. T. 1990. Potential lifetime fecundity and the factors affecting annual fecundity in *Urodacus armatus* (Scorpiones, Scorpionidae). J. Arachnol., 18:271–280.

van Berkum, F. H. 1982. Natural history of a tropical, shrimp-eating spider (Pisauridae). J. Arachnol., 10:117–122.

Werner, E. E. & J. F. Gilliam. 1984. The ontongentic niche and species interaction in size-structured populations. Ann. Rev. Ecol. Syst., 15:393–425.

Werner, E. E., D. J. Hall & G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology, 64:1540–1548.

Wilbur, H. M. 1980. Complex life cycles. Ann. Rev. Ecol. Syst., 11:67–93.

Zimmermann, M. & J. R. Spence. 1989. Prey use of the fishing spider *Dolomedes triton* (Pisauridae, Araneae): an important predator of the neuston community. Oecologia, 80:187–194.

Manuscript received 31 August 1994, revised 11 November 1994.