
Short Communication

Sexual Differences in Behavioral Response to Conspecifics and Predators in the Wolf Spider *Gladicosa pulchra* (Aranea: Lycosidae)

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Accepted February 10, 1993; revised April 22, 1993

KEY WORDS: Lycosidae; *Gladicosa pulchra*; habitat change; sexual differences; conspecifics; predators.

INTRODUCTION

Discrete habitat changes involving trade-offs between foraging and risk of mortality occur during the life cycle of many animals, and interactions with conspecifics and predators are among the important biological factors thought to influence such changes (Werner and Hall, 1988; Wilbur, 1980; see review by Werner and Gilliam, 1984). Recent work has focused on the effects of predators on habitat selection, and one of the principal conclusions of this work is that animals possess the ability to assess and behaviorally control their risk of predation (see review by Lima and Dill, 1990). Numerous laboratory and field studies have clearly demonstrated that exposure to predators induces changes in behavior associated with habitat choice and foraging in many animal species (Werner *et al.*, 1983; Dixon and Baker, 1988; Gotceitas and Colgan, 1990).

Considerably less attention, however, has been given to the importance of intersexual interactions in habitat changes. Even though sexual differences have been documented for habitat use in aquatic isopods (Jormalainen and Tuomi, 1989), antipredator mobbing behaviors in birds (Sordahl, 1990), and mortality due to predation (Gwynne, 1987), the majority of the extensive work regarding habitat changes in animals has ignored sexual differences. Most authors have elected to use juvenile fish (Gotceitas, 1990; Gotceitas and Colgan, 1990) or larval stages of insects (Pierce, 1988; Dixon and Baker, 1988) to study predator-

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mediated habitat use and have not investigated the roles that sexual differences may play in these habitat changes. Abrahams and Dill (1989) have provided evidence that male and female guppies forage differently in the presence of predators and that sexual differences in the energetic equivalence of the risk of predation exist. However, their experiments were not designed to test hypotheses concerning sexual differences and therefore the conclusions that can be drawn from them are limited.

The objective of this study was to test explicitly for sexual differences in a habitat change as a result of interactions with conspecifics and predators. We performed a series of field experiments to determine if either density of conspecifics, sex of conspecifics, or density of predators influenced a habitat change in male and female *Gladicosa pulchra* (Keyserling) (Lycosidae) wolf spiders.

MATERIALS AND METHODS

Study Organisms. The nocturnal wolf spider *G. pulchra* undergoes a habitat change in the late summer or early fall that involves movement of predominately penultimate and adult individuals from forest floor to tree trunk habitats (Eubanks and Miller, 1992). Our previous study of the natural history and ecology of this species (Eubanks and Miller, 1992) suggested that interactions with both conspecifics and predators could be important proximate influences on tree climbing behavior and that males and females differed in their tree climbing behavior. Male spiders initiated tree climbing as both penultimates and adults early in the season, whereas female spiders initiated tree climbing primarily as adults later in the season. Both adult males and females are found almost exclusively on trees in the fall months (88% of 208 observations). Spiders return to the forest floor with the onset of winter, where females overwinter gravid and produce egg sacs while occupying burrows during the spring. Adult males do not overwinter and are not found at the study site during spring and early summer. *G. pulchra* were never collected on trees smaller than 2 cm in diameter, whereas over 65% of the trees at the site are smaller than 2 cm in diameter. The studies detailed below were conducted in September and October of 1990 in a mixed hardwood forest located on the campus of the University of Mississippi in Oxford (Lafayette County), where *G. pulchra* occur in large numbers. Spiders used in the experiments were collected at the site and held in the laboratory for 1 to 21 days prior to each experiment. The long holding times were required to allow immature spiders to reach maturity. All spiders were fed house crickets, *Acheta domesticus*, ad libitum and provided ample water. Large individuals (mature or penultimate females) of the wolf spider, *Lycosa georgicola* Walckenaer, were used as the predator in the experiments. *L. georgicola* occurs in great numbers at the study site and during the tree climbing phase of *G. pulchra* individuals of this species are roughly twice as large as individuals of *G. pulchra*

(Eubanks and Miller, unpublished data). Individual *L. georgicola* prefer leaf litter habitats and occasionally ascend into the low branches of understory shrubs and saplings. We have previously documented that *L. georgicola* individuals rarely climbed trees as large as those preferred by *G. pulchra* (approximately 1% of > 100 observations of these spiders) (Eubanks and Miller, 1992).

Intraspecific Density Experiments. In order to test the effects of sex, density, and their interaction on habitat selection by *G. pulchra*, we constructed six 60-cm-radius experimental arenas by burying logs vertically and surrounding them with 15-cm-high aluminum flashing, with 1.5 m of the log exposed above ground to produce an "artificial" tree. Logs were used instead of "natural" trees to control the height that spiders could climb and diameter of trees and are referred to as trees throughout this paper. Leaf litter was removed from within the experimental arena to facilitate observations of spiders. Trees were selected to have a diameter of 8 cm, which is within the size range preferred by *G. pulchra* (Eubanks and Miller, 1992). The experiment consisted of scoring the tree climbing behavior (dichotomous dependent variable, climbed/did not climb) of a male or female focal spider when subjected to varying densities and sexes of conspecifics in the arena. Focal spiders were marked with correction fluid on one femur for identification and placed into the experimental arena. Pilot studies indicated that marking did not effect behavior (Eubanks, 1991). Male or female conspecifics were then randomly assigned to the experimental arena at one of four densities: 0 (focal spider alone in the arena; control) or 1, 2, and 3 additional spiders in the arena. Each combination of focal sex, conspecific sex, and conspecific density was replicated three times in this factorial design. The focal spider and conspecifics (if any) were placed in the arena equidistant from one another and 30 cm from the tree 2 h before sunset. Observations were made at sunset and hourly for 4 h with a headlamp. At each observation, we recorded whether the focal spider or conspecifics climbed the tree and determined whether all spiders were still present in the arena. Since only six test arenas were available each night, density treatments were randomized by night. All trees and the aluminum flashing were thoroughly cleaned with a water-moistened sponge after each use in an effort to remove any silk left behind by previous occupants.

Predation Pressure Experiments. In order to test the effects of predator density on habitat selection by male and female *G. pulchra*, we manipulated the density of female *L. georgicola* inside experimental arenas that contained male or female *G. pulchra*. The arenas used in the intraspecific density experiments were used in this series of experiments. In these experiments, the climbing behavior of focal male or female *G. pulchra* was observed while exposed to four different densities of *L. georgicola*: 0 (focal spider only; control) and 1, 2, and 3 *L. georgicola* individuals in addition to the focal spider. These densities were similar to those observed at the study site (Eubanks and Miller, 1992). The spiders were placed equidistant from one another and approximately 30 cm

from the tree 2 h before sunset, and observations were made as described in the intraspecific density experiments. Each predator density was replicated three times for each sex in this factorial design and randomized over 4 nights as described above.

Analysis. Logistic regression analysis (Hosmer and Lemeshow, 1990) was used to delineate relationships between the dichotomous dependent variable (climbed/did not climb) and the set of discrete predictor variables including sex of the focal spider, sex of conspecifics (intraspecific density experiment), density of conspecifics or predators, and presence or absence of a conspecific on the tree (intraspecific density experiment). Logistic regression analysis tests for hierarchy in the importance of the set of predictor variables. The G statistic ($df = 1$), was used to test whether models that include subsets of the predictor variables are superior to the full model including the entire set and all interactions among the predictors. The likelihood ratio, D , analogous to the residual sum of squares in linear regression, is reported and the test statistic G is used to determine which model is the most appropriate. Logistic regression analysis was calculated using the BMDP statistical package.

RESULTS

Intraspecific Density. Significantly more male focal spiders than female focal spiders climbed trees in the presence of conspecifics ($G = 6.49$, $D = -14.54$, $df = 1$, $0.025 > P > 0.01$) (Fig. 1). Neither the density nor the sex of additional conspecifics had a significant effect on the number of males or females that climbed trees ($G = 1.51$, $D = -12.05$, $df = 1$, $0.5 > P > 0.1$, and $G = 2.51$, $D = -12.552$, $df = 1$, $0.5 > P > 0.1$, for density and sex, respectively); however, males were significantly more likely to climb trees already inhabited by one or more conspecifics ($G = 8.2$, $D = -22.67$, $df = 1$, $0.005 > P > 0.001$).

Predation Pressure. Significantly more female focal spiders than male focal spiders climbed trees in the presence of predators ($G = 7.94$, $D = -11.077$, $df = 1$, $0.005 > P > 0.001$, interaction of focal spider sex and predator density) (Fig. 2). No *L. georgicola* climbed trees during the experiments.

DISCUSSION

In this study, males climbed trees significantly more often than females in the presence of conspecifics and significantly more often than females when a conspecific was already on the tree. Females climbed trees significantly more often than males in the presence of forest floor predators. Although many alternative explanations to interpret these sexual differences in behavioral response to conspecifics and predators could be proposed, three logical hypotheses seem

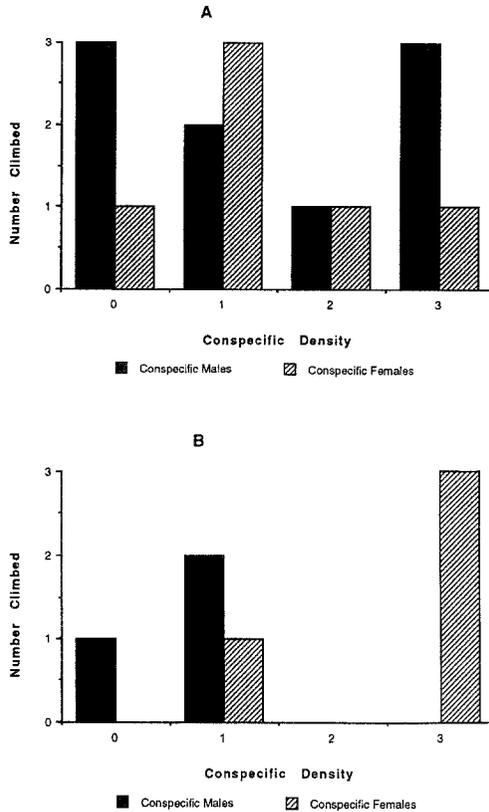


Fig. 1. Results of the intraspecific density experiments. (A) Number of male focal spiders that climbed trees in the presence of male (filled bars) and female (hatched bars) conspecifics. (B) Number of female focal spiders that climbed trees in the presence of male (filled bars) and female (hatched bars) conspecifics. Conspecific density increases from left to right.

the most plausible: (1) male and female *G. pulchra* have different sensory abilities; (2) male and female *G. pulchra* perceive components of predation risk differently; and (3) female *G. pulchra* climb trees to avoid forest floor predators, and males climb trees to find females (i.e., male behavior is a consequence of female behavior). It is important to point out that these three hypotheses may not be mutually exclusive, but for convenience we address each independently.

The first two hypotheses proposed seem the most unlikely to explain our results. Dramatic sexual differences in sensory ability have not been reported for wolf spiders (Foelix, 1982), and laboratory and field observations of male

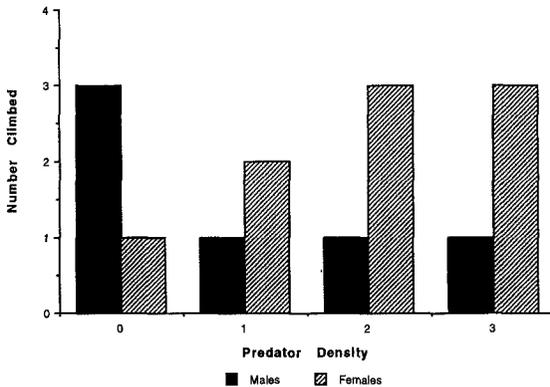


Fig. 2. Results of the predation pressure experiments. Number of male and female focal spiders that climbed trees in the presence of predators. Filled bars show the number of male focal spiders that climbed trees and hatched bars show the number of female focal spiders that climbed trees. Predator density increases from left to right.

and female *G. pulchra* responding to stimuli such as prey items (crickets, moths, etc.) indicate that such differences do not exist (Eubanks, 1991). Nor is it likely that male and female *G. pulchra* perceive components of risk differently, i.e., distance to safety, maximum speed the animal can travel, time exposed to predators, probability of escape, etc. Authors have proposed that animals deal with problems of risk perception by using simple "rules" that reflect their evolutionary history of predation (Lima and Dill, 1990). For example, Sih (1986) demonstrated that larvae of a mosquito species (*Culex pipiens*) that commonly cooccurs with a predator (*Notonecta undulata*) had far stronger behavioral responses to predators than larvae of a mosquito species (*Aedes aegypti*) that does not commonly cooccur with a predator. Male and female *G. pulchra* may have different rules owing to different mortality rates due to predation. However, our observations during this and our previous study (Eubanks and Miller, 1992) did not indicate that female *G. pulchra* have higher mortality rates than males due to predation. Our experimental results indicate the opposite, that males have a higher mortality rate (one instance of predation in conspecific density experiment and one instance of predation in predator density experiment) than females (no instances of predation in either experiment), but males are less sensitive to predators, not more sensitive as other studies would predict (see discussion by Lima and Dill, 1990).

The presence of forest floor predators elicited tree climbing behavior in female *G. pulchra*, a result that is consistent with other studies demonstrating

that animals change or utilize habitats to avoid predators (Lima and Dill, 1990). Male *G. pulchra* spiders climbed trees significantly more often than females in the presence of conspecifics on the ground and climbed trees significantly more often when a conspecific was already on the tree. During the predator density experiments *G. pulchra* males were in the experimental arena with only the predator *L. georgicola*, therefore no conspecifics were on the tree, and males did not climb trees in significant numbers. These results are consistent with the hypothesis that females use trees to avoid forest floor predators and males use trees to locate conspecifics. We do not know if male spiders climb trees that have already been climbed by other spiders in response to cues such as pheromones, although this behavior would correspond to male drag-line following in other lycosid species (Tietjen and Rovner, 1980). Our experimental design allowed us to analyze the effect of additional conspecifics that climbed the tree prior to the focal spider on tree climbing behavior. We did not, however, manipulate the number of additional conspecifics that climbed the tree, nor did we manipulate the presence/absence of cues such as pheromones. Experimental manipulations to address the effects of these conditions may provide further insight into the tree climbing behavior of *G. pulchra*. Although we have not observed courtship and copulation in this species, the abundance of penultimate and mature spiders found on trees in our previous study (Eubanks and Miller, 1992) suggests the importance of the arboreal habitat in the reproduction of this species. It is likely that males climb trees to find female conspecifics, i.e., potential mates, and not conspecifics in general. To test this idea fully, future studies should focus on experiments in which the sex of conspecifics already present on trees is manipulated, in conjunction with descriptive work on the mating system of this species. Obviously, more observational and experimental work is needed before we fully understand the tree climbing behavior of this species, but our results are consistent with the hypothesis that these sexual differences are related to life history characteristics of individual *G. pulchra*, with females using tree habitats to avoid forest floor predators and males using tree habitats to locate potential mates.

ACKNOWLEDGMENTS

We thank T. G. Forrest for the many comments made on early drafts of this paper and for his lengthy discussions on this subject. B. Benrey, R. F. Denno, H. G. Dobel, C. R. Figiel, P. M. Leddy, J. E. Losey, J. C. Trexler, and two anonymous reviewers provided constructive comments on an early draft of the manuscript. This study was funded by a grant from the Exline-Frizzell Fund for Arachnological Research, California Academy of Science.

REFERENCES

- Abrahams, M. V., and Dill, L. M. (1989). A determination of the energetic equivalence of the risk of predation. *Ecology* **70**: 999–1007.
- Brady, A. R. (1986). Nearctic species of the new wolf spider genus *Gladicosa* (Aranea: Lycosidae). *Psyche* **93**: 285–319.
- Dixon, S. M., and Baker, R. L. (1988). Effects of size on predation risk, behavioural response to fish, and cost of reduced feeding in larval *Ischnura verticalis* (Coenagrionidae: Odonata). *Oecologia (Berlin)* **76**: 200–205.
- Eubanks, M. D. (1991). *Effects of Intraspecific Competition and Predation Pressure on a Habitat Change in the Wolf Spider Gladicosa pulchra (Keyserling)*, M.S. thesis, University of Mississippi.
- Eubanks, M. D., and Miller, G. L. (1992). Life cycle and habitat preference of the facultatively arboreal wolf spider, *Gladicosa pulchra* (Araneae, Lycosidae). *J. Arachnol.* **20**:157–164.
- Foelix, R. F. (1982). *Biology of Spiders*; Harvard University Press, Cambridge, MA.
- Gotceitas, V. (1990). Foraging and predator avoidance: A test of a patch choice model with juvenile bluegill sunfish. *Oecologia (Berlin)* **83**: 346–351.
- Gotceitas, V., and Colgan, P. (1990). The effects of prey availability and predation risk on habitat selection by juvenile bluegill sunfish. *Copeia* **1990**: 409–417.
- Gwynne, D. T. (1987). Sex-biased predation and risky mate-locating behaviour of male tick-tock cicadas (Homoptera: Cicadidae). *Anim. Behav.* **35**: 571–576.
- Hosmer, D. W., and Lemeshow, S. (1990). *Applied Logistic Regression*, John Wiley and Sons, New York.
- Jormalainen, V., and Tuomi, J. (1989). Sexual differences in habitat selection and activity of the colour polymorphic isopod *Idotea baltica*. *Anim. Behav.* **38**: 576–585.
- Lima, S. L., and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.* **68**: 619–640.
- Pierce, C. L. (1988). Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia (Berlin)* **77**: 81–90.
- Sih, A. (1986). Antipredator responses and the perception of danger by mosquito larvae. *Ecology* **67**: 434–441.
- Sordahl, T. A. (1990). Sexual differences in antipredator behavior of breeding American avocets and black-necked stilts. *Condor* **92**: 530–532.
- Tietjen, W. J., and Rovner, J. S. (1980). Trail following behavior in two species of wolf spiders: Sensory and etho-ecological concomitants. *Anim. Behav.* **28**: 735.
- Werner, E. E., and Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**:393–425.
- Werner, E. E., and Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology* **69**:1352–1366.
- Werner, E. E., Gilliam, J. F., Hall, D. J., and Mittelbach, G. G. (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. *Annu. Rev. Ecol. Syst.* **11**: 67–93.