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LIFE CYCLE AND HABITAT PREFERENCE OF THE FACULTATIVELY ARBOREAL WOLF SPIDER, *GLADICOSA PULCHRA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. The life history and habitat preference of the wolf spider *Gladicosa pulchra* were investigated in several populations in Mississippi. *Gladicosa pulchra* has a one year life cycle with spiders changing from forest floor to tree trunk habitats in late summer or early fall. During the fall, spiders were found almost exclusively on trees (93% of observed spiders in 1989 and 80% of observed spiders in 1990). Males were observed to inhabit trees earlier in the year than females. Spiders did not climb trees smaller than 2 cm in diameter at breast height. Most individuals were collected at heights less than 2.5 m, and spiders were primarily oriented face down while on trees. The role that environmental factors play in this animal's habitat preference is discussed.

Although the wolf spiders (Lycosidae) are primarily ground dwellers, some species are occasionally found on low vegetation (e.g., *Lycosa carolinensis* Walckenaer, *L. timuqua* Wallace, and *L. rabida* Walckenaer, Kuenzler 1958; Barnes 1953, *L. hentzi* Banks, Miller et al. 1988), small low tree branches (e.g., *L. rabida*, Kuenzler 1958), and, less often, the trunks of trees (e.g., *L. hawaiiensis* Simon, Gon 1985). One species for which the use of arboreal habitats appears to be a more significant aspect of its life history is *Gladicosa pulchra* (Keyserling). Brady (1986) reported that mature males and females of this species were commonly collected from the trunks of trees but rarely from the forest floor. Miller and Miller (pers. obs.) have found the extensive use of tree trunk habitats during certain times of the year predominately by penultimate and mature individuals in both pine and hardwood habitats in Florida and Mississippi. These observations, particularly the dearth of sightings of individuals in habitats other than trees, imply that *G. pulchra* spiders may undergo an abrupt habitat change, moving from forest floor to trees. However, no detailed ecological study of this species has been undertaken, and the phenology and significance of the use of arboreal habitats are unclear. In particular, it is not known whether tree trunk habitats serve primarily as sites for foraging, reproduction, or as a refuge from predators.

The purpose of this study was to delineate the life cycle of *G. pulchra* for the purpose of understanding the importance of the use of the arboreal habitat in this species. In particular, we describe (1) the life history, (2) the timing of tree climbing behavior, (3) tree size preference, (4) height of spiders on trees, (5) the orientation of spiders on trees, and (6) sex differences in arboreal habitat use.

METHODS

Habitat Preferences and Life History.—We conducted the study in a 3 ha mixed-hardwood woodlot located on the University of Mississippi campus, near Oxford (Lafayette County), Mississippi. The study site was composed predominantly of a canopy and understory of *Quercus* spp. with abundant leaf litter (> 15 cm depth in some locations). We made weekly nighttime surveys of the area between 30 March–19 November 1989, and between 1 February–15 October 1990. Periodic observations were made during February, June, and July of 1991, but no measurements were made. For every individual *G. pulchra* observed on a tree we determined: (1) the diameter [cm] at breast height [DBH] of the tree, (2) the height [cm] of the spider on the tree, (3) the vertical orientation of the spider measured as degrees to the nearest 10° with face down orientation designated as 0°, and (4) the number of additional *G. pulchra* spiders on the tree. All spiders that were collected in 1989 and 1990

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were taken to the laboratory where immatures were reared to adulthood to assess sex and developmental stage at capture; however, not all spiders that were observed were collected.

To determine the size distribution of trees in the woodlot we measured the DBH of every tree within 2 m of three north–south transects (each 200 m in length). The transect samples represented approximately 4% of the area of the woodlot. Weekly average temperatures and rainfall accumulations were obtained from the USDA National Sedimentation Laboratory weather station located approximately five km from the field site in Oxford, Mississippi.

In addition to the detailed observations made at the primary study site, we made periodic observations (approximately once each month) at four other areas of Lafayette County, Mississippi. We propose a life history of this species based on all of our observations in all study areas.

Statistical Analyses.—To determine whether individual *G. pulchra* select trees of a specific size, we compared the size (DBH) distribution of trees climbed by spiders to that of trees sampled along the transects with a Kolmogorov-Smirnov (KS) goodness-of-fit test (test statistic designated d_{max}; Sokal & Rohlf 1980). Regression analysis was employed to determine if there was a seasonal trend in the DBH of trees selected by spiders. A two-tailed Durbin-Watson test was used to determine whether the error terms of the regression were uncorrelated (Neter et al. 1991). The two-tailed test is performed by testing separately for positive and negative autocorrelation where the Type I error for the combined test is 2α (Neter et al. 1991).

We tested whether the orientation of males and females was uniformly distributed around a circle using the Rayleigh test (test statistic denoted Z; Zar 1984). The mean direction, the 95% confidence interval of the mean, the Z statistic, and, r, a unitless measure of magnitude or concentration that ranges from 0 (indicating so much dispersion that a mean direction cannot be described) to 1.0 (where all the data are concentrated at the same direction) are presented (Zar 1984).

Contingency table analysis (G-statistic, Sokal & Rohlf 1980) was used to compare the frequency with which adult male and female, penultimate male and female, and immatures were present on trees during each year. We employed logistic regression analysis (Hosmer & Lemeshow 1989) to determine if the sex of a spider was related to the date collected, height of the spider at the time of collection, or the DBH of the tree on which the spider was observed. Logistic regression analysis is used to test for relationships between a discrete (usually dichotomous) dependent variable and discrete or continuous independent (predictor) variables. In our analysis the presence or absence of females represented the dichotomous dependent variable and the variables DBH, height of collection site, and date of collection or observation represented the predictor variables. A hierarchy of models including all subsets of the independent variables was examined. The likelihood ratio (denoted D), which is analogous to the residual sum of squares in linear regression, is reported and the test statistic G was employed to determine what variables were significant predictors of the response variable (Hosmer & Lemeshow 1989). Logistic analysis was calculated on the BMDP statistical package.

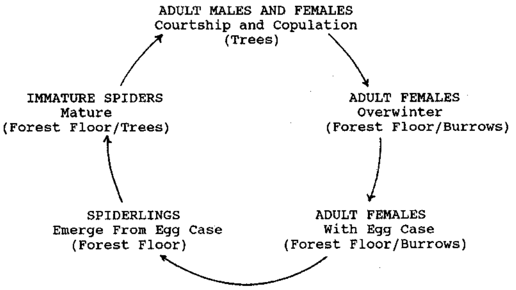

Figure 1.—Proposed life history of *Gladicosa pulchra*. Adults are present on trees in the fall of the year where courtship and copulation is thought to occur. Females overwinter gravid and produce egg cases in the spring while inhabiting burrows. Females move about on the forest floor with spiderlings on their abdomen in late spring. Spiders then climb trees as they approach maturity during the late summer and early fall.

Student's *t* test was used to determine if the average DBH of trees occupied by more than one spider was larger than the average DBH of trees occupied by a single spider. To determine if there were seasonal differences in the number of trees occupied by more than one spider, we used logistic regression as described above with the number of spiders per tree as the dependent variable. Because of the small number of sampling dates during 1991, we did not attempt to analyze seasonal trends for that year.

Table 1.—Summary of collections of *G. pulchra* for 1989 and 1990. The (*) indicates that males and females were not reared to adulthood to access sex, and the (**) indicates that immatures were not included in the totals.

	On trees		On forest floor	
	Males	Females	Males	Females
1989—(30 Mar.–19 Nov.) (*n* = 91)				
Immature	0	4	0	0
Penultimate	18	14	0	1
Adult	6	43	1	4
Total	24	61	1	5
1990—(1 Feb.–15 Oct.) (*n* = 153)				
Immature	56*	—	18*	—
Penultimate	16	13	5	0
Adult	18	20	3	4
Total	34**	33	8**	4

RESULTS

Life History.—A proposed life history of *G. pulchra* is diagrammed in Fig. 1. During 1989 and 1990, adult males and females were collected predominantly on trees in the fall. Courtship and copulation were not observed during either year, however, during February of 1991 we collected two gravid females. These females were found in vertical burrows approximately 10 cm deep each with a turret constructed of leaf litter. During this same month, three mature females and one immature spider were collected from the forest floor and a mature female was taken from a tree at another site located on the University of Mississippi, Oxford campus. Patricia Miller (pers. comm.) observed a mature female with an egg sac occupying a burrow located in her yard 1.2 km north of Oxford, Mississippi. This burrow had a turret constructed from grass. During both census years, no adult males were collected during the spring.

Habitat Preferences.—Of the 91 spiders collected during 1989 headlight censuses, 6 (7%) were found on the forest floor (Table 1). Only one, an adult female, was collected prior to 21 August, the first date that spiders were collected from trees (Table 1). The first date that spiders were collected from trees coincided with the first week of the year during which the average weekly temperature reached 29 °C or higher in both 1989 and 1990 (21 August 1991 and 2 June 1991, respectively).

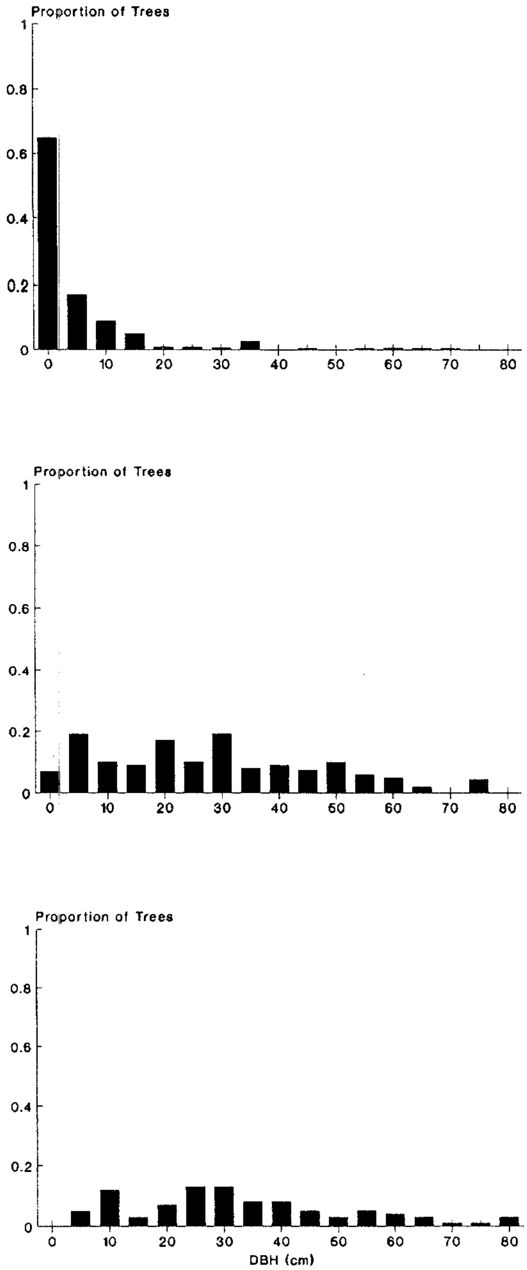

Figure 2.—Top, Frequency of occurrence of trees in sixteen, 5 cm size classes (Diameter in cm at Breast Height) for trees selected along transects; Middle, trees climbed by spiders in 1989; and Bottom, trees climbed by spiders in 1990.

The average DBH of trees selected along the transects was 8 cm (*n* = 196, SD = 19; Fig. 2), and that distribution of tree sizes also differed significantly from the distribution of trees se-

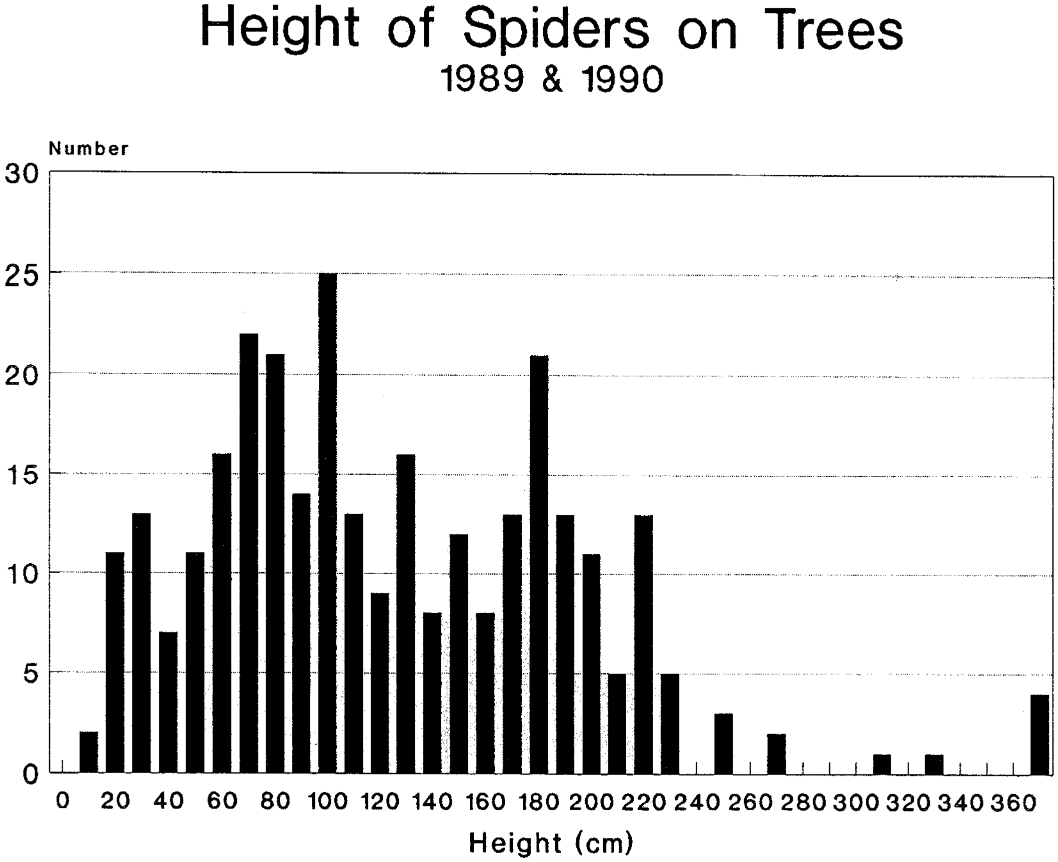

Figure 3.—The number of *Gladicosa pulchra* collected at each height (cm) on trees during 1989 and 1990 at the study site on The University of Mississippi campus, Oxford, Mississippi.

lected along the transects (KS test, $d_{max} = 0.64$, $n_1 = 90$, $n_2 = 196$, $P < 0.01$).

The two-tailed Durbin-Watson test for autocorrelation revealed no positive or negative correlation among error terms in the regressions of DBH against collection date for either 1989 or 1990 (test for positive correlation, $D_{1989} = 1.663$, $n = 180$, $D_{1990} = 1.814$, $n = 108$, $P < 0.01$; test for negative correlation, $D_{1989} = 6.656$, $n = 180$, $D_{1990} = 2.186$, $n = 108$, $P < 0.01$). There was no seasonal change in tree size preference during 1989 or 1990 (Regression analysis, $R^2 = 0.02$, MSE = 518.89, $df = 139$, $P > 0.05$; $R^2 = 0.02$, MSE = 360.32, $df = 89$, $P > 0.10$, 1989 and 1990 respectively).

In 1989, 93% of the 91 spiders collected were found on trees (Table 1). Adult females were found significantly more often on trees than any other sex/stage combination in 1989 (contingency table analysis, $G_{adj} = 17.79$, $n = 85$, $P < 0.001$). During the 1990 census, 80% of the 153 spiders collected were found on trees. In 1990 no sex/stage combination was present significantly more often than any other (contingency table analysis, $G_{adj} = 0.37$, $n = 67$, $P > 0.5$). Immature spiders were first collected from trees on 2 June 1990, and 85% of the 13 spiders collected on that date were on trees. Adult spiders were not collected on trees until late August, as in 1989.

The height of spiders on trees averaged 145 cm in 1989 and 80 cm in 1990. No seasonal changes in height were observed during either year (Regression analysis, $R^2 = 0.02$, MSE = 3979.55, $df = 89$, $P > 0.05$; $R^2 = 0.04$, MSE = 5549.43, $df = 107$, $P > 0.05$, 1989 and 1990 respectively). During both years most spiders were at heights below 2.5 m (Fig. 3).

During both years the vertical orientation of spiders differed significantly from random, with most individuals adopting a face down position on the tree (mean direction = 0°, $n = 101$, 95%

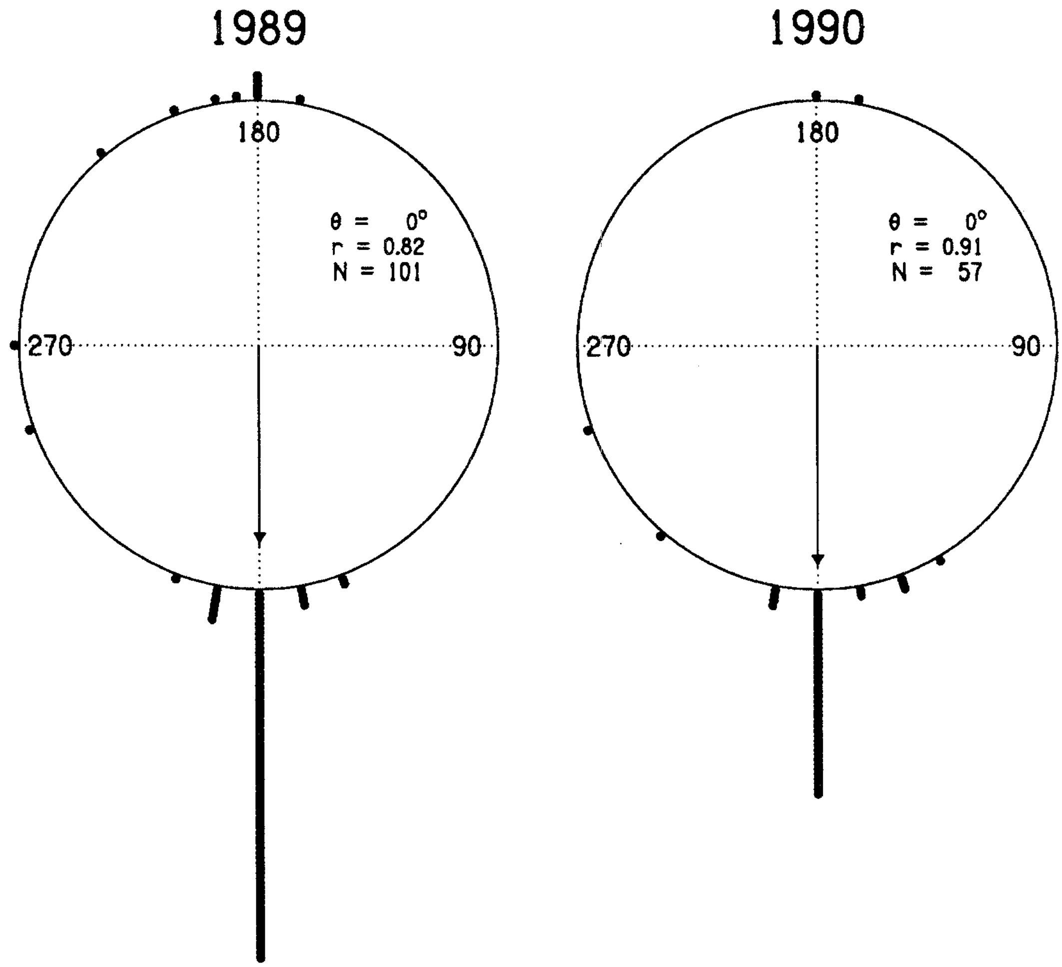

Figure 4.—Orientation of *Gladicosa pulchra* collected from trees in 1989 and 1990. Figures show the mean direction (P), magnitude (r), and number of observations (*N*), 0° = facing down. Each darkened circle represents two observations.

CI ±10, r = .82, Z = 67.91, $P < 0.001$; mean direction = 0°, $n = 57$, 95% CI ±10, r = 0.91, Z = 47.20, $P < 0.001$; 1989, 1990 respectively; Fig. 4). Males, females, and immatures all had mean directions = 0°.

The proportion of spiders collected or observed during 1989 that were female was 0.73, significantly different from a 1:1 male/female sex ratio (χ^2, $P < 0.001$). Logistic regression analysis results showed that date was the best predictor of the sex of an individual spider (D = −56.246, G = 8.81, $0.005 < P > 0.001$). Female spiders were more likely to be found on trees later in the season than males. In 1990, the overall proportion of females in the population was 0.47 and did not differ significantly from a 1:1 male/female sex ratio (χ^2, $P > 0.05$). In 1990, date was the best predictor of the sex of an individual spider collected from a tree (D = −20.554, G = 9.2, $0.005 < P > 0.001$), and as in 1989, females were more likely to be found later in the season than males.

During both years few spiders were observed to occupy trees that contained other *G. pulchra* (16 out of 238 observations, 7%). During 1989 trees occupied by a single spider had a significantly smaller mean DBH than those with two or more spiders ($t = -4.53$, $P < 0.001$), but not in 1990 ($t = 0.1$, $P > 0.05$). The number of trees occupied by more than one spider at one time significantly increased during the season in 1989 (D = −26.451, G = 12.881, $df = 6$, $P < 0.05$), but this was not the case during 1990 ($D = -22.040$, $G = 10.013$, $df = 7$, $P > 0.1$).

DISCUSSION

Although we collected immature individuals during February of 1991, we believe that the observations reported here support the suggestion of a one-year life cycle for *G. pulchra*, with courtship and copulation occurring in the fall (Fig. 1). Although the location of courtship and copulation is uncertain, the abundance of penultimate and mature spiders found on trees in the fall of 1989 and 1990 suggests the possible importance of the arboreal habitat in the reproduction of this species. Females apparently overwinter gravid and produce egg sacs in burrows during the spring. It is unclear whether females construct burrows or whether they usurp completed or partially completed burrows of another species. It is evident, however, females expend some energy in the construction and maintenance of the turret.

Spiderlings emerge from egg sacs in the spring and reach sexual maturity during the early fall. Once the spiderlings emerge, the female abandons the burrow and wanders about the forest floor carrying the young on her abdomen in the manner typical of non-burrowing wolf spiders. Adult males apparently do not overwinter, and are present predominantly on trees during the fall.

Our observations showed that in 1989 and 1990 *G. pulchra* is present primarily on trees during the late summer and early fall. Spiders were rarely collected from the forest floor or from trees prior to the fall, but females were found in burrows during the spring. These observations suggest that individuals move from the forest floor (either from burrows or from the leaf litter) to trees during the late summer or early fall. Previous studies of spiders have documented variations in microhabitat use by different sizes or different life stages of conspecifics (e.g., Waldorf 1976; Hallander 1970). Hallander (1970) reported that spiders of the genus *Pardosa* stratified their use of leaf litter habitats according to body size in order to limit the effects of cannibalism. However, the change from the forest floor habitat to a tree dwelling life style observed in *G. pulchra* is substantially more dramatic than most habitat shifts observed in spiders. Animals may change habitats to balance the conflicting demands of minimizing the risk of mortality and maximizing food intake (e.g., Werner & Gilliam 1984, Werner et al. 1983, Gilliam & Fraser 1987, Werner & Hall 1988, Pierce 1988, Gotceitas & Colgan 1990, Gotceitas 1990) or to avoid intraspecific competition or size-specific predation (Werner & Gilliam 1984). The relative importance of these two factors in the habitat change of *G. pulchra* will be reported elsewhere.

In both 1989 and 1990 adult females and penultimate males were occasionally observed to occupy positions on the same tree. The asynchrony in the timing of maturation of males and females that is indicated by these observations is not uncommon in spiders (e.g., Austin 1984; Berry 1987; Miller & Miller 1987). Such differences in the timing of maturation may lead to pre-courtship cohabitation (e.g., Robinson & Robinson 1980; Christenson & Goist 1979; Pollard & Jackson 1982; Jackson 1977; Miller & Miller 1986). Typically, if cohabitation occurs, the mature male seeks a stationary subadult female and waits with her until she matures. However, our observations indicate that penultimate males ascend trees earlier in the year than females, which typically climb as adults. Thus, if the proximity of males and females on trees represents pre-courtship cohabitation in this species, then both the behaviors associated with the phenomenon (e.g., one sex moving to locate another) and the relative timing of the maturation of the sexes are different from that observed in other spiders. It is important to note that the proximity of males and females of different stages on the same tree may be the result of other processes (e.g., foraging, predator avoidance) not related directly to reproductive behavior. Moreover, the majority of our observations were of single individuals on a tree (see below).

Our observations indicate that the onset of tree climbing in *G. pulchra* is not exclusively triggered developmentally. The sex ratio of collected spiders was strongly female biased in 1989, but not in 1990. Additionally, the beginning of the tree dwelling phase came later in the year in 1989 than in 1990. In 1990, spiders climbed trees earlier in the year (June vs. August) and earlier in their life cycle (immature vs. penultimate or adult). Thus, spiders climbed trees at different stages in the two years. Although, considerably more work will be required to determine the relative influence of physical and biological factors in this behavior, our study suggests the importance of rainfall as a critical physical parameter. Total rainfall was greater in the summer of 1989 than in the summer of 1990. Humidity and soil moisture should be directly influenced by rainfall, and these two factors have been shown to play an important role in the microhabitat selection of spiders (Cady 1984; Reichert & Tracy 1975).

Individual *G. pulchra* were never collected on trees smaller than 2 cm DBH during this study. Larger trees may provide larger foraging areas or refuge from forest floor predators. We have no information about the relative availability of prey on trees and the forest floor, but spiders were often observed feeding on ants and moths on trees. However, a potential predator of *G. pulchra*, the large wolf spider *Lycosa georgicola* Walckenaer, is common on the forest floor. We have seen individuals of that species climb small saplings but we made only a single observation of *L. georgicola* on a tree larger than 2 cm DBH.

The average height of spiders on trees did not change as the season progressed in 1989 or 1990. Spiders were predominantly found at heights between 1.5–2.5 m, and individuals of all stages (immatures, penultimates, and adults) typically adopted a face down orientation while on the tree. In the absence of a compelling physiological explanation for the face-down behavior, we suggest that such an orientation is the most practical for intercepting prey and/or mates that originate from below. The relatively constant height through the season supports this notion.

Although we observed trees that held more than one spider, most of the spiders seen during this study were the lone occupant of the tree from which they were collected. Many field studies have established that density-dependent effects, such as competition for web sites, occur in web-building spiders (Schaefer 1978; Reichert 1979; Wise 1981). Web-building spiders tend to stratify web construction in a manner that reduces competition. Our observations may indicate an analogous form of habitat stratification or territoriality.

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