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January 1998

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Miller, Gary L.; Stratton, Gary L.; Miller, Patricia R.; and Hebets, Eileen, "Geographical variation in male courtship behavior and sexual isolation in wolf spiders of the genus *Schizocosa*" (1998). *Eileen Hebets Publications*. 25.

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Geographical variation in male courtship behavior and sexual isolation in wolf spiders of the genus *Schizocosa*

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Abstract

We surveyed 12 populations of the wolf spider *Schizocosa crassipes* (Walckenaer) and *S. nr. crassipes* in Tennessee, Mississippi, Louisiana, and Florida, in the United States, to determine the extent of variation in male courtship behavior when observed in standard laboratory conditions. We observed variation in both the frequency of occurrence and the sequence of the four principal male courtship behaviors and, when compared statistically, most of these behaviors differed between populations. Although there was no clinal pattern in the frequency of courtship behavior, we observed geographically consistent patterns in the sequence in which male courtship behaviors are displayed. We conducted two subsequent studies to determine whether sexual isolation among selected populations existed. In the first study, we performed male-female reciprocal crosses of brush-legged spiders (*S. nr. crassipes*) between two populations from the Yazoo-Mississippi Delta physiographical region and one population from the Loess Bluff region of Mississippi and measured mating success, number of matings that produced egg sacs, and the number of egg sacs that hatched young. The results of that experiment suggest that sexual isolation occurs among populations in different physiographical regions but not between populations within regions of the state. In a second crossing study, we paired the brush-legged spiders from one of the Mississippi physiographical regions (Yazoo-Mississippi Delta) with *Schizocosa ocreata* (Hentz) from Ohio. The results of that cross suggest that the Mississippi Delta population is more similar to the northern *S. ocreata* populations than to *S. crassipes*. We discuss the results of the crossing experiments in terms of what was revealed about geographical patterns in male courtship behavior.

Sexual and/or reproductive isolation has been proposed as an important step in the evolutionary differentiation of populations leading to speciation. Groups in which this has been observed include *Drosophila* (e.g. Kaneshiro 1976; Watanabe & Kawanishi 1979; Wasserman & Koepfer 1980; Markow 1981; Moodie 1982; Spieth & Ringo 1983; Eherman & Wasserman 1987; Koepfer 1987; Coyne 1989, 1993; Krebs & Markow 1989), lacewings (Futuyma & Mayer 1980; Henry 1983; Henry *et al.* 1993; Tauber & Tauber 1997a, b), salamanders (Houck *et al.* 1988; Verrell 1989; Verrell & Arnold 1989), and spiders (Stratton & Uetz 1981, 1983; Schmidt 1990). The questions of principal interest turn on what evolutionary processes give rise to sexual isolation, what genetic mechanisms underlie the process and what behavioral mechanisms maintain isolation.

Understanding the nature of geographical variation in behavior, particularly courtship behavior, is essential to answering these questions. Genetic divergence arising from selection for adaptations to local environments among allopatric populations and genetic drift may lead to sexual isolation when such divergence is correlated with behavior (Mayr 1963; Koepfer 1987). Behavioral differences in newly sympatric populations that have undergone genetic divergence might undergo reinforcement (Dobzhansky 1970) thereby strengthening isolation. This has been demonstrated in laboratory selection studies with *Drosophila* (e.g. Wasserman & Koepfer 1977; Ringo *et al.* 1985). Isolation may also occur in sympatric subpopulations that have adapted to different microhabitats or in races of organisms adapted to different hosts (e.g. Bush 1992; Feder *et al.* 1994; Schlieffen *et al.* 1994; review by

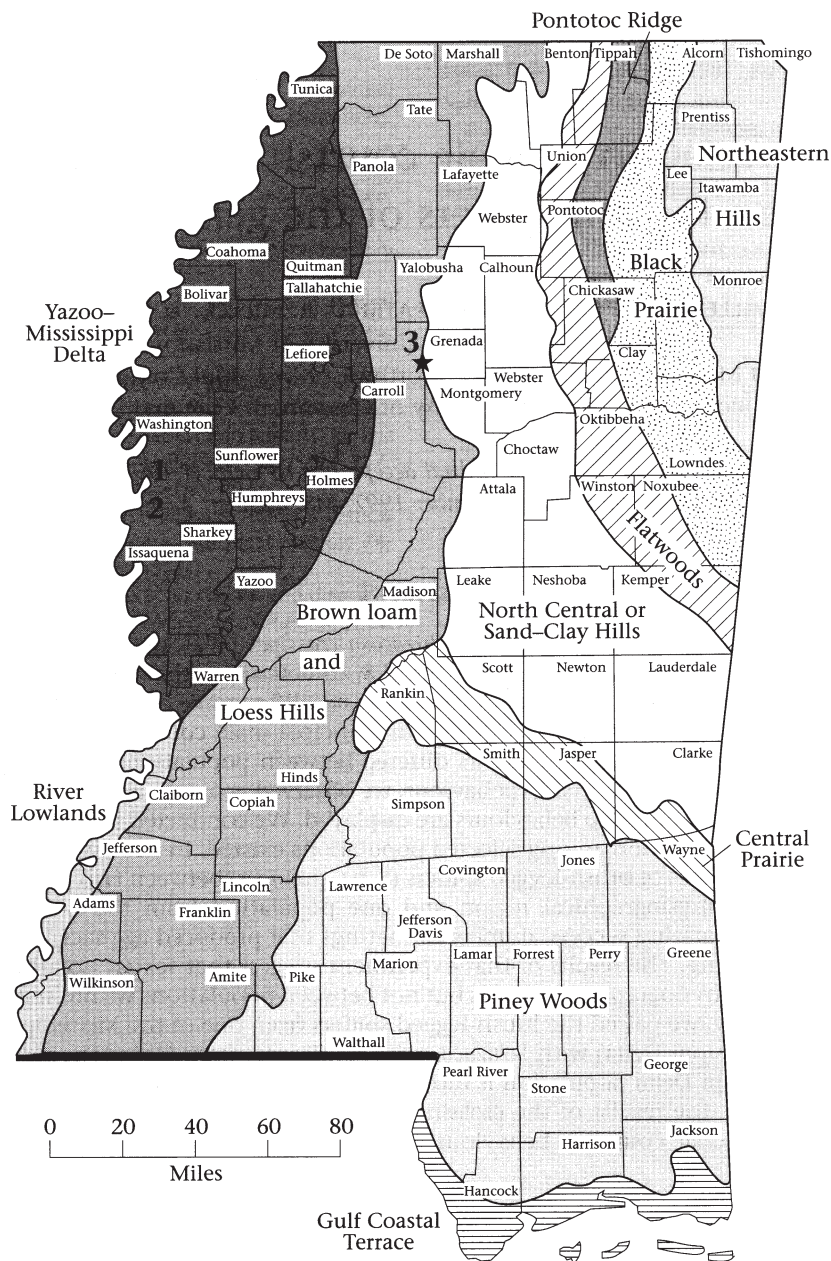


Figure 1. Map of the state of Mississippi showing the location of three populations of *Schizocosa* nr. *crassipes* examined in the sexual isolation study. 1 = Stoneville Woods, 2 = Leroy Percy State Park (1 and 2 in Yazoo-Mississippi Delta physiographical region), 3 = Grenada (Loess Bluffs region).

Bush 1994). Multilocus genetic simulation models suggest that sympatric reproductive isolation may occur under a wide variety of conditions (Johnson *et al.* 1996). Clues to the mechanism of speciation and whether speciation is occurring sympatrically or allopatrically, can be obtained from comparisons of the temporal and sequential components of courtship behavior exhibited between and within populations of geographically widespread groups (Markow 1981; Markow & Hanson 1981; Welbergen *et al.* 1987; Verrell & Arnold 1989). Such studies have the potential to reveal not only the geographical pattern of species differentiation, and thus the importance of underlying geolog-

ical processes, but also the importance of specific behavioral patterns in the process of speciation.

Here we report on three studies. The first was undertaken to determine the extent of variation in male courtship behavior among 12 populations of the forest floor wolf spiders that appear to be *Schizocosa crassipes* and *Schizocosa* nr. *crassipes* in the southeastern U.S.A. Two other experimental studies were undertaken to determine whether sexual reproductive isolation exists among selected populations occurring in two distinctly different physiographical regions in Mississippi (Yazoo-Mississippi Delta and Loess Bluffs; see Figure 1) and between a

Mississippi population from the Yazoo-Mississippi Delta region and a population of the cryptic species *S. ocreata* from Ohio. The studies revealed that among populations: (1) the courtship behavior of male *S. nr. crassipes* varies both in the frequency of occurrence of the principal displays, and in the sequence in which the displays are given during a courtship bout; (2) although male courtship displays differ among populations, there is no overall geographical pattern of variation in male courtship behavior; (3) sexual isolation exists between populations in two regions of Mississippi; and (4) one population from Mississippi appears to be less strongly sexually isolated from *S. ocreata* in Ohio than from *S. crassipes* in a nearby but different physiographical region of Mississippi.

Study Species

Schizocosa (Araneae, Lycosidae) is a nearctic genus of wolf spider. Some members of the genus have conspicuous secondary sexual characteristics; all species studied to date have distinctive and conspicuous courtship that involves the use of pheromones, acoustic/vibrational, and, possibly, visual signals (Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983, 1986; Uetz & Stratton 1982; Stratton & Lowrie 1984; Hebets *et al.* 1996). These spiders are keen sighted and do not build webs to capture prey. They are important as predators in many ecosystems (Wise & Wagner 1992).

Sibling species are common in wolf spiders (e.g. Tanaka & Suwa 1986). The genus *Schizocosa* contains at least two species groups that have cryptic species (*S. ocreata* group, the subject of this study; *saltatrix* group, G. Miller, P. Miller and G. Stratton, unpublished data), and it appears that, in general, the genus is diversifying more by behavioral changes and changes in secondary sexual characteristics than by the changes in the genital morphology seen in many other arthropod genera (Eberhard 1985). For example, within the members of the *S. ocreata* (Hentz) species group, which includes *S. ocreata*, *S. crassipes* (Walckenaer), *S. rovneri* Uetz and Dondale, *S. floridana* Bryant, *S. stridulans* Stratton and *S. uetzi* Stratton, male palpal morphology and epigynal morphology vary little among species (Dondale & Redner 1978; Uetz & Dondale 1979; Stratton 1991, 1997a, b). There are, however, recognizable differences in male secondary sexual characteristics of these species and male courtship behavior is divergent among groups.

Our focus has been on *S. crassipes* and *S. ocreata*, and a number of closely related yet undescribed species, the mature males of which have prominent, darkly pigmented, bristles on the first pair of legs, which apparently have an epigamic function. Both species have been called "brush-legged" spiders. The brush-legged species present a particularly challenging systematic problem because of the similarity of their morphology (Dondale & Redner 1978) and the complexity of their courtship behavior. While northern populations of *S. ocreata* have been studied extensively (e.g. Aspey 1977; Stratton & Uetz 1981, 1983, 1986; Wise & Wagner 1992; Scheffer *et al.* 1996; Uetz *et al.* 1996), few behavioral and ecological studies have focused on the more southern *S. crassipes*. A third species, *S. rovneri*, occurs in

portions of the geographic range of both brush-legged spiders (Stratton 1991). The genital morphology of the mature males of this species is identical to that of the *S. ocreata*, but males of *S. rovneri* lack the brushes and employ principally substrate-borne stridulation in their courtship behavior (Stratton & Uetz 1981, 1983).

Many populations of brush-legged spiders, which occupy a variety of habitats throughout the southeastern U.S.A., are intermediate between *S. crassipes* and *S. ocreata* with respect to reported morphological characteristics and habitat preferences. Thus, the systematic affinities of each population was unknown at the outset of this study. We undertook this study to characterize the courtship behavior of *S. nr. crassipes*, to investigate the courtship patterns of populations of brush-legged spiders throughout the southeastern U.S.A. in order to document the divergence in these species, and to investigate the degree of sexual isolation between selected populations.

GEOGRAPHICAL VARIATION IN MALE COURTSHIP

Methods

Collection and video observation

Schizocosa *nr. crassipes* were collected at 12 locations in Tennessee, Mississippi, Louisiana, and Florida (Table 1, Figure 2) in the spring of 1993 and taken to our laboratory at the University of Mississippi in Oxford, Mississippi. All populations were located in hardwood or mixed pine-hardwood deciduous forest. Spiders were collected from the leaf litter. With the exception of specimens taken at the Grenada, Mississippi, site, where we collected spiders just after their last moult, we collected only immature or penultimate-stage spiders. All spiders were held in the laboratory in individual containers, provided water *ad libitum*, and fed one or more appropriately sized crickets at least once each week. Temperature in the laboratory ranged from 22° to 26°C. Spiders were kept on 14:10 h light: dark cycle.

To determine the basic male courtship pattern for each population, we made a series of observations according to the following protocol. At least 12 hours prior to each trial, we removed mature, virgin females from their holding cages and placed them on clean filter paper in a culture dish 8 cm in diameter. We fed each female one cricket of an appropriate size. Just prior to a trial, we transferred the female and her filter paper to a cylindrical observation chamber, 6 cm in diameter. The filter paper was arranged so that a small portion protruded through a slit at the base of the container; the protruding portion of the filter paper served as the contact for a sound transducer attached to an EG&G PARC Model 113 pre-amp (EG&G Princeton Applied Research, Wellesley, Massachusetts) for the recording of substrate-borne male stridulations. For males that showed courtship, we obtained 10–15 min of video recordings of the displays using a Panasonic WD-5000 camera with KIRON 105 mm f/2.8 macrolens 1:1 lens (Secaucus, New Jersey). In most cases, only the male was videotaped. Courtship bouts that resulted in copulation

Table 1. Summary of collection sites for video studies of male courtship behavior of brush-legged *Schizocosa crassipes*, and *S. nr. crassipes*. Locations are arranged north to south

State, location and habitat		Number of males observed	Number of courtships recorded
Tennessee Mississippi	Henderson Co., Natchez Trace State Park, pine deciduous leaf-litter	6	4
	Grenada Co., deciduous uplands leaf-litter hills and ravines	20	11
	Washington Co., Leroy Percy State Park, bottomland hardwood leaf-litter	46	23
	Washington Co., Stoneville Woods, bottomland hardwood leaf-litter	8	4
	Sharkey Co., flooded bottomland hardwood leaf-litter	1	1
	Claiborne Co., deciduous uplands leaf-litter hills and ravines	4	4
	Adams Co., Natchez State Park, deciduous uplands leaf-litter on hillside	3	2
	Wilkinson Co., deciduous uplands leaf-litter on hillside	23	9
Louisiana	Calcasieu Parish, Sam Houston Jones State Park, pine deciduous litter near cypress swamp	27	9
	Natchitoches Parish, deciduous leaf-litter	10	5
Florida	Alachua Co., Loch Loosa; (area recently logged) in deciduous litter along creek	10	5
	Alachua Co., River Styx, pine deciduous litter bottomland	15	5

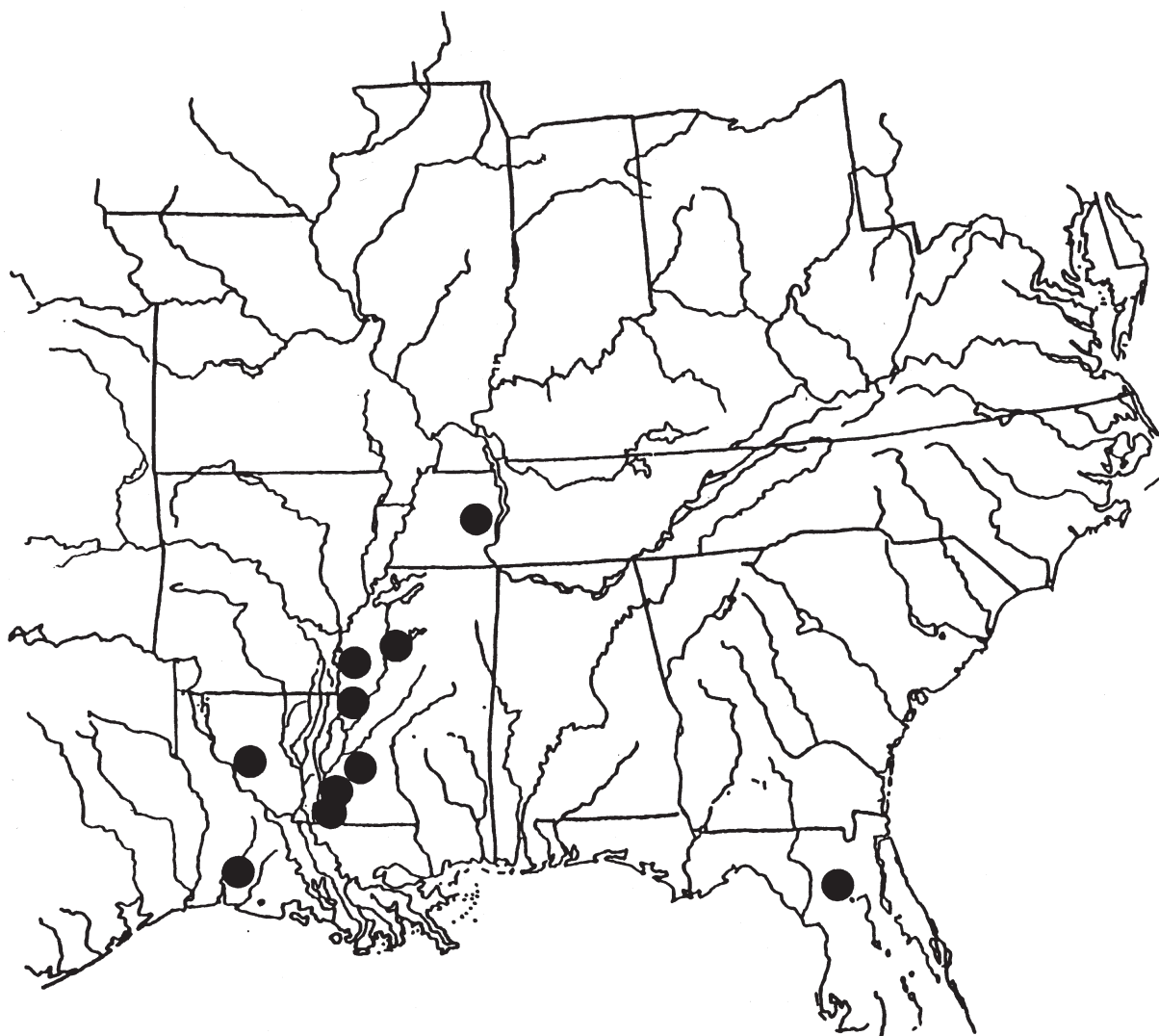
**Figure 2.** Map of the southeastern United States showing collection locations for the study of geographical variation in male courtship behavior of *Schizocosa nr. crassipes*.

Table 2. Description of male courtship and female receptive behavior of *S. nr. crassipes*

Behavior	Description of behavior
Male behaviors	
Bounce	This involves a rapid and forceful slamming of the body to the substrate. In <i>S. rovnerei</i> , it appears that the abdomen strikes the surface before any part of the cephalothorax. In <i>S. nr. ocreata</i> , the fangs appear to be the first contact point. The mechanism for the bounce is unclear. At the time the body makes contact with the surface all legs and the palps are lifted. (Similar to the bounce behavior described by Stratton & Uetz 1986, except that there is no evidence of stridulation during bounce as they suggest for <i>S. rovnerei</i>).
Extension	Extension, occasionally with rapid tapping, of one or both first legs. Usually given while standing and in close proximity to female. (Similar to "double tap" of Stratton & Uetz 1986).
Arch	An arching of one or more legs above cephalothorax in such a way that, for each leg arched, the femur, patella-tibia and metatarsus-tarsus form a right angle. An arch may involve the first leg and/or second leg of one or both sides and may include gentle tapping on the substrate while in the arch position.
Wave	Similar to arch except that the leg is extended at the metatarsus. While extended, the legs are waved rapidly above the cephalothorax.
Female behaviors	
Pivot	The female pivots clockwise or anticlockwise half to one-third of a turn. Body held low. Generally performed in front of a stationary male. Usually involves several turns.
Settle	Lowering of the body accompanied by soft leg taps.
Wave	Very slow wave of the first pair of legs while positioned in front of the male.

Differences in terminology from that used by Stratton & Uetz (1986) are noted where appropriate.

were allowed to proceed until the end of copulation. In most cases, a portion of the copulation was also videotaped for another study (Stratton *et al.* 1996).

One observer selected 2-min segments of uninterrupted courtship, and then a second observer scored each segment for the frequency and sequence of occurrence of the principal behaviors. The observer who scored the tapes was unaware of the population being scored. Following the procedure of Adano & Hoy (1994), we included for analysis only behaviors that represented 15% or more of the total behaviors given during a 1-min observation period to avoid unacceptably low cell frequencies in subsequent statistical analysis. Four such behaviors were observed (Table 2). Although it is possible that behaviors that occur less frequently may be important in female recognition, our main purpose in this study was to compare the overall male pattern between populations as an indication of geographical variation in courtship behavior.

Homogeneity of observations

Prior to undertaking an interpopulation comparison of the frequency distributions and the sequence of the male courtship displays among populations, it was necessary to make two preliminary determinations. To ensure that a random selection of a 2-min courtship bout was appropriate, and to see how consistent individual males were, we asked whether the frequency of occurrence of male courtship behaviors changes with time during long courtship bouts. For males having lengthy (>6 min) courtship displays, we selected two or more non-overlapping 2-minute segments of courtship and scored the frequency of occurrence of the behaviors for each of these segments (these were presented to the scorer out of sequence and intermixed with repeated sequences of other males). Using the G test for homogeneity among repeated observations (Sokal & Rohlf 1995), we compared the repeated sequences of each male (Table 3).

For those males for which there was no significant difference in the frequency of occurrence of the courtship behavior between repeated 2-min segments of the same bout, we used the average of the 2-min bouts observed to represent that male in further analyses. No repeated observations were made on the spiders from the Florida populations owing to the short courtship bouts recorded. In all cases except three (two males from Claiborne County, Mississippi, and one male from Sharkey County, Mississippi), the frequency of occurrence of the principal displays was invariant over the length of the courtship bout. We deduce from these results that a random choice of a 2-min scoring segment is acceptable. Males that did not show temporal homogeneity in frequency of courtship display were excluded from all further analysis.

In a second analysis, we asked whether the males within each population were homogeneous in the frequency of occurrence of their courtship displays. This information was necessary because at the outset of the study we did not know the scale at which species differentiation might occur. Our previous experience with forest floor wolf spiders suggested that the appropriate scale might be quite fine and that the possibility existed for differences in courtship to occur in a local population. Our examination of intrapopulation variation in the frequency of courtship display revealed a high degree of homogeneity in all but two populations (Natchez Trace Park, Tennessee, and Claiborne County, Mississippi; Table 4). Two distinct groups of males were observed at the Leroy Percy, Mississippi, site (3 males per group). These are designated Leroy Percy I and Leroy Percy II, and for the purposes of the analysis of frequency distributions of male courtship, are analyzed as separate populations. No significant difference in the frequency distributions of male behaviors was observed between males within any of the other populations.

Table 3. Homogeneity of repeated observations of selected males

Population	Male	Number of repeated observations	G test for homogeneity among repeated observations		
			G	df	P<
Natchez Trace, Tennessee	531	2	1.741	3	0.628 NS
	541	2	2.103	3	0.551 NS
Grenada, Mississippi	495	3	2.507	6	0.868 NS
Sharkey, Mississippi	601	2	1.569	3	0.666 NS
	597	2	11.444	3	0.010**
Claiborne, Mississippi	145	2	9.953	3	0.019**
	150	2	10.005	3	0.019**
Homochitto, Mississippi	656	2	5.372	3	0.146 NS
	648	2	1.091	3	0.770 NS
Sam Houston, Louisiana	679	2	3.678	3	0.298 NS
Dogwood, Louisiana	743	2	2.528	3	0.470 NS

Each 2-min bout was randomly selected from lengthy (>6 min) courtship sequences. No repeated sequences were scored from the two Florida populations owing to the short duration of the courtship bouts observed in males of those populations.

Table 4. G statistic analysis of intrapopulation homogeneity of male courtship behavior

Population	G	df	P	Group size (no. males)
Natchez Trace, Tennessee	11.54	3	<0.05	No homogeneous groups of males, 2
Grenada, Mississippi	7.67	6	NS	
Leroy Percy, Mississippi I	6.65	3	NS	
Leroy Percy, Mississippi II	1.33	3	NS	2
Stoneville, Mississippi	6.85	6	NS	3
Sharkey, Mississippi	6.04	6	NS	3
Claiborne, Mississippi	17.91	6	<0.05	No homogeneous groups of males, 3
Homochitto, Mississippi	3.40	6	NS	
Natchez, Mississippi	5.14	3	NS	
Sam Houston State Park, Louisiana	8.84	9	NS	4
Dogwood Trails, Louisiana	4.93	6	NS	3
Loch Loosa, Florida	5.21	6	NS	3
River Styx, Florida	4.52	6	NS	3

Homogeneous sets are shown for populations where there was more than one set. Two groups of homogeneous males (each with two males) were observed at Leroy Percy State Park. These are designated Leroy Percy I and II.

Analysis of frequency distributions of male courtship display

We employed a replicated goodness-of-fit analysis (Sokal & Rohlf 1995) to examine differences in the frequency distributions of male courtship behaviors between the populations where the populations were viewed as replicates. The analysis involved the following steps. First, for each population, we tested (log-likelihood method, G test) the hypotheses of a uniform distribution of courtship behaviors (Table 5). The uniform distribution was employed because it is the most parsimonious and no other plausible distribution has been suggested. This analysis revealed that some populations differed from the expected distribution and others did not (Table 5). To determine the extent of departure from expectation for the group of populations as a whole, we calculated the total G statistic, which is the sum of the individual population G statistics. A significantly high total G statistic suggests that there is heterogeneity among

populations in the frequency of occurrence of behaviors when compared to the expected frequency. We then calculated the pooled G statistic from the pooled frequency data from all populations to determine whether the trend in the departure from the expected was the same in all populations. If the departures from the expected frequency distribution between the populations compensated for one another in some way (*e.g.*, one group of populations had high frequencies of Bounce and Extension and low frequencies of Arch and Wave, and another group of populations had low frequencies of Bounce and Extension and high frequencies of Arch and Wave; see Table 2), we would expect a small pooled G. Finally, to determine whether the magnitude of the departure from expected was similar among populations, we calculated the heterogeneity G statistic. If populations that differed from expected did so with the same magnitude, we would expect a low value for this statistic.

Table 5. Average frequency of occurrence of four courtship behaviors, and the test of the hypothesis of a uniform frequency distribution of the behaviors in 12 populations of *Schizocosa* nr. *crassipes* in Tennessee, Mississippi, Louisiana, and Florida

Population	Behavior				G	P
	Bounce	Extension	Arch	Wave		
Natchez State Park, Tennessee	(No homogeneous groups with more than one male)					
Grenada/Mississippi	9.6	10.5	9.3	7.8	0.41	NS
Leroy Percy State Park, Mississippi I	34.5	32	8	1	55.75	**
Leroy Percy State Park, Mississippi II	48.5	29	21	15	21.49	**
Stoneville, Mississippi	11	9.3	16	4	7.85	NS
Sharkey, Mississippi	39.6	45.0	21.8	1.6	57.94	**
Claiborne, Mississippi	(No homogeneous groups with more than one male)					
Homochitto National Forest, Mississippi	10	13	14.2	3.3	8.46	*
Natchez State Park, Mississippi	13	10.5	14	4.5	5.98	NS
Sam Houston Jones State Park, Louisiana	4.4	12.5	16.5	2.5	15.71	**
Dogwood Trails, Louisiana	13.2	13.5	15.8	8	2.77	NS
Loch Loosa, Florida	15	36	22	9	19.46	**
River Styx, Florida	12	21	20	7	9.64	**

Averages are among groups of males having homogeneous frequency distributions. Two such groups (two males each) were observed at the Leroy Percy, Mississippi site. * $P < 0.05$; ** $P < 0.001$; NS: $P > 0.05$.

Analysis of the sequence of male display

To delineate patterns in the sequence of male courtship behaviors within and between populations, we constructed a transition matrix of preceding and following behaviors for each population using the methods of Dingle (1969) and Clark (1994). We performed an analysis of each transition matrix by first calculating a χ^2_9 value for the entire matrix to determine whether “preceding” behaviors were independent of “following” behaviors. For all matrices for which the independence of preceding and following behaviors was rejected, we calculated the row χ^2 . The presence of row χ^2 values greater than 11.34 ($P < 0.01$; here we follow the conservative approach advocated by Clark 1994) indicates the possibility of significantly different behavioral dyads (*i.e.*, a pair of behaviors that occur more or less frequently together than expected if pairs of behaviors were chosen at random). To identify significant behavioral dyads (reported in Table 6), we calculated the cell χ^2 values using the equation of Clark (1994), which adjusts the cell degrees of freedom to 1. We assumed that behaviors that occurred significantly more frequently than expected for a particular following behavior would facilitate following behavior, whereas behaviors that occurred significantly less frequently than expected would inhibit following behavior.

Voucher specimens from all of these studies are deposited at the Mississippi Entomological Museum at Mississippi State University.

Results

Frequency distributions of display

The distributions of relative occurrence of the principal male courtship behaviors are shown in Figure 3, and the absolute frequencies for each population are shown

in Table 5. The analysis of these distributions indicated that in seven of the 12 populations, the frequency distribution of displays differed from the hypothesized uniform distribution, and there was significant heterogeneity among populations in the way in which they departed from the expected uniform distribution ($G_{\text{total}} = 205.46$). The pooled data departed significantly from the expected frequency ($G_{\text{pooled}} = 58.74$) indicating that, although populations were heterogeneous in their departure from expected, the pattern of the departure was similar across populations. While the pattern of departure among populations was the same, the magnitude of the departure differed ($G_{\text{heterogeneity}} = 146.75$).

Populations differed in which behavior was most common. Arch occurred most frequently in five of the 11 populations for which groups of homogeneous males were observed. Extension and Bounce were observed most frequently in four and two of the populations, respectively. In four of the populations (Grenada, Stoneville, Natchez, Mississippi, and Dogwood Trails, Louisiana), the null hypothesis that the principal behaviors would occur at the same frequency within a 2-min courtship bout was not rejected. In the other populations, one or more of the displays was observed more frequently than the others. For the northern populations (Leroy Percy I and II, and Sharkey), Bounce and Extension behaviors occurred more frequently than Arch or Wave displays, whereas in the more southern populations (Homochitto, Mississippi; Sam Houston Jones, Louisiana; Loch Loosa and River Styx, Florida), the rejection of the null hypothesis of uniformity resulted from either considerably fewer Wave displays per bout relative to the other three behaviors (e.g. Homochitto and the two Florida populations) or significantly more Extension and Arch behaviors relative to Bounce and Wave behaviors (e.g. Sam Houston Jones State Park, Louisiana).

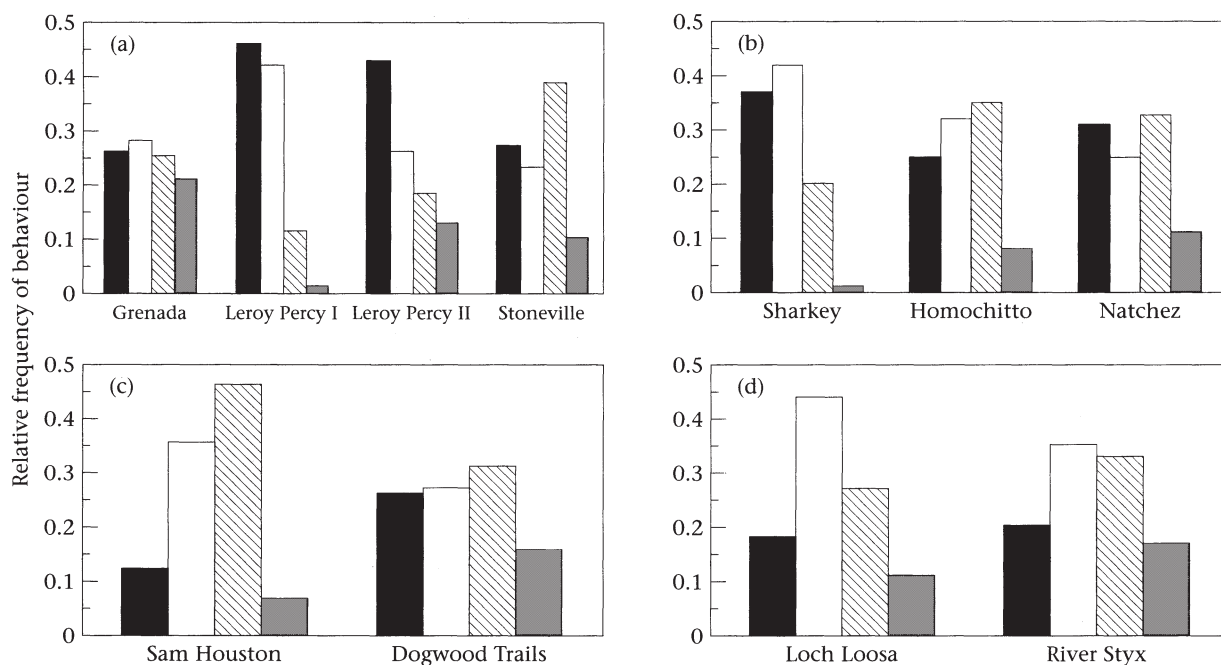


Figure 3. Relative frequency of display of male courtship behaviors for each of 12 populations of *Schizocosa nr. crassipes* in the southeastern U.S.A. (a) Northern Mississippi populations; (b) Southern Mississippi populations; (c) Louisiana populations; and (d) Florida populations. ■: Bounce; □: Extension; ▨: Arch; ■: Wave.

Table 6. Significant behavioral dyads from the transition matrices of male courtship behavior in 12 populations of *Schizocosa nr. crassipes*.

Population	Behaviors that facilitate following behavior				Behaviors that inhibit following behavior			
	Bounce	Extension	Arch	Wave	Bounce	Extension	Arch	Wave
Natchez Trace, Tennessee								
Grenada, Mississippi				A	A	E		
Leroy Percy, Mississippi I				B				B
Leroy Percy, Mississippi II								
Stoneville, Mississippi	W	A	E					
Sharkey, Mississippi	E	A	B		A			
Claiborne, Mississippi								
Homochitto, Mississippi	B,W	A	E		A	E		
Natchez, Mississippi	B,W		E		A			
Sam Houston Jones, Louisiana	B,W		E		A	E		
Dogwood Trails, Louisiana	B,W		E		A,E	E		
Loch Loosa, Florida	W		E		—	—	—	—
River Styx, Florida	W	W	W	W	—	—	—	—

B=Bounce, E=Extension, A=Arch, W=Wave. No inhibiting behaviors were found in the two Florida populations.

Sequence of display

The transition matrix of preceding and following behaviors, along with the population (entire population matrix) and row χ^2 values are presented for each population in the Appendix. A significant total χ^2 was observed for each population indicating nonindependence of preceding and following behaviors in each population. In all but two of the populations (Leroy Percy II and Stoneville) significant row χ^2 values were observed in at least one row of the population matrix, indicating the possible presence of significant behavioral dyads.

The analysis of the significant rows suggests the presence of a geographically consistent pattern in the temporal

sequence of male courtship behavior (Table 6). Behaviors that facilitate each of the four courtship displays studied here were consistent, with two exceptions (*i.e.*, the facilitating behavior for Bounce and Arch in Sharkey County and the facilitating behavior for Extension and Arch in River Styx), the facilitating behaviors were the same across all populations for each of the four male displays. Bounce was facilitated both by Wave and by Bounce or by Wave alone (e.g. Stoneville). Extension was always facilitated by Arch and Arch by Bounce. We observed a similar interpopulation consistency in inhibiting behaviors. For all populations where significant dyads were observed, Bounce was inhibited by Arch, and Extension was inhibited

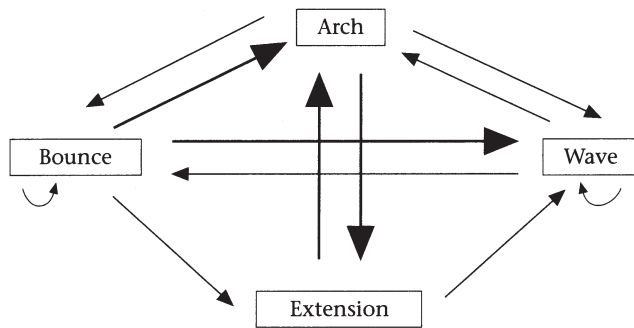


Figure 4. General sequence of behaviors in the male courtship of *Schizocosa* spiders. Arrows point towards behaviors that are facilitated. Heavy lines indicate the most common situation (i.e. more than one significant dyad; see Table 6). Thin lines indicate uncommon patterns of behavior (i.e. a single significant dyad; see Table 6).

by Extension (indicating that Extension behaviors are rarely repeated in a 2-min courtship bout). Based on these results, we propose a generalized model of the sequence of behavior (Figure 4).

Discussion

The analysis of successive segments of male courtship in lengthy male courtship bouts and the test of infra-population variation in male display indicated the presence of considerable homogeneity in male courtship within most of the populations that we examined. The exception to this was the Leroy Percy site, where males having two different courtship frequency distributions were observed. These results suggest that, generally, local variation in male courtship behavior is not pronounced.

We analyzed two types of male courtship information: the frequency of display of each behavior relative to other important behaviors and the sequence in which displays are presented to the female. Our results revealed considerable interpopulation variation in the first type of information and little variation in the second type. With respect to the sequence of male courtship, we observed the biggest differences in the pattern of facilitation of the Grenada, Mississippi, and Natchez Trace, Tennessee, populations compared with other populations. These results suggest that different selective or environmental pressures affect these two types of courtship information.

The male courtship behavior of wolf spiders is extremely complex, and it is likely that our analysis, which was intended to elucidate broad geographical patterns, lacked the resolution to diagnose subtle differences in the courtship of males from different populations. The Arch and Wave behaviors, although distinctive, are often given with variable amounts of speed and vigor, which may alter the information content of these displays. We have preliminary evidence of differences in the response of males to the pheromones of females from their own and different populations. Moreover, there are considerable interpopulation differences in microhabitat structure, population density, diurnal behavior, and the intensity of male-male

interactions (G. Miller, G. Stratton, P. Miller, personal observation), which are excluded from our laboratory analysis of behavior, but which may have a strong influence on the pattern of male courtship behavior in the field.

The scale of the variation in male courtship behavior may depend on habitat heterogeneity, the intensity of microhabitat preferences, local and geographical dispersal patterns, and genetic difference among populations. If distinctive microhabitats exist within the normal population range of a species, divergent courtship types could arise if there is disruptive selection on traits related to microhabitat preference (a hypothesized mechanism of sympatric speciation; e.g., Tauber & Tauber 1977a,b; Rice & Salt 1990; Bush 1994). This idea also merits further investigation in this group.

SEXUAL ISOLATION

Methods

Collection and video observation methods

Spiders used in the first sexual isolation experiments were collected in 1995 from three Mississippi locations (Figure 1). Leroy Percy State Park and Stoneville Forest, both bottomland forests in Washington County, are situated approximately 48 km apart in the Yazoo-Mississippi Delta physiographic region of the state. A third population in Grenada County is located in deciduous woods on the Loess Bluffs of central Mississippi. For the second sexual isolation experiment in 1996, we collected *S. ocreata* from Hamilton County, Ohio, and *S. nr. crassipes* from Leroy Percy State Park, Mississippi. All spiders were collected in the penultimate instar and thus were virgins for this experiment.

The videotaping procedures for the sexual isolation experiments were similar to those used for the study of the geographical variation in male courtship except that (1) both the male and the female spider were included in each video recording, and (2) because we were interested principally in whether mating would occur, the length of the taping bout was determined by the activities of the spiders, with a single bout lasting until the beginning of copulation or until 10 min after the beginning of the bout, whichever came first.

Experimental design for sexual isolation studies

To determine whether sexual isolation exists among three Mississippi populations located in two distinct physiographic regions (Yazoo-Mississippi Delta and Loess Bluffs; Figure 1), and to discover whether there is asymmetry of sexual isolation if isolation exists, we employed a crossing experiment in which mature male and female spiders from the same (homotypic) and different (heterotypic) populations were paired and their behaviors were videotaped. For each population pair (Grenada-Leroy Percy; Grenada-Stoneville; Leroy Percy-Stoneville), we observed 20 heterotypic male-female pairings. In each case, 10 of the heterotypic pairings involved a female from the population and 10 involved a male. For example, in the

Table 7. Comparison of homotypic and heterotypic matings of Mississippi *Schizocosa* in the spring and summer of 1995. Means (\pm SD)

Population		No. crosses attempted	No. copulations observed	No. producing egg sac	No. egg sacs hatching eggs	Mean time (days) to	
Male	Female					Egg sac	Hatching
Gr	Gr	10	5	5	4	24.6 (17.0)	32 (0.0)
Gr	St	10	0	—	—	—	—
Gr	LP	10	0	—	—	—	—
LP	LP	10	8	7	7	12.9 (2.9)	30.4 (0.5)
LP	St	10	8	6	5	19.2 (18.9)	32.0 (11.2)
LP	Gr	10	0	—	—	—	—
St	St	10	8	8	7	12.3 (6.8)	30.5 (0.5)
St	LP	10	8	8	8	12.1 (4.3)	30.0 (0.0)
St	Gr	10	1	1	1	11 (0.0)	34 (0.0)

Spiders were collected on April 13–14, 1995, as immatures and penultimates and were maintained in the laboratory at 25°C and on a LD 14:10h cycle.

Gr = Grenada, St = Stoneville and LP = Leroy Percy.

case of Grenada-Stoneville, 10 of the pairings involved Grenada females and Stoneville males and 10 of the pairings involved Grenada males and Stoneville females. We conducted 10 homotypic pairings for each population.

We performed a second, similar, series of pairings in 1996 to determine whether populations of *S. nr. crassipes* from the Yazoo-Mississippi Delta region are fully reproductively isolated from *S. ocreata*. We performed seven Ohio-Ohio pairings and six Leroy Percy-Leroy Percy pairings. We also performed 12 Ohio male-Leroy Percy female pairings and 12 Ohio female-Leroy Percy male pairings.

Mating success

We noted whether copulation occurred (successful mating) and whether egg sacs were produced. We estimated the binomial parameter separately for the homotypic encounters combined and the heterotypic encounters combined by setting 95% confidence intervals on P , the ratio of the number of successful matings to the total number of encounters attempted (an estimator of the binomial parameter). We counted the number pairings resulting in the production of egg sacs and the number of those egg sacs from which eggs hatched for both the Mississippi crosses and the Mississippi-Ohio crosses. In the case of the Mississippi crosses, we also determined the time from egg sac production to hatching.

Results

Sexual isolation among Mississippi populations

Homotypic encounters resulted in matings over 80% of the time (binomial test: 95% confidence limits for all homotypic encounters combined: 0.49, 0.84, $N = 30$, $P = 0.71$; Table 7). Females of the Leroy Percy and Stoneville populations, the two Mississippi Delta populations, were unable to distinguish homotypic and heterotypic males from those populations; nearly all of the pairings (8 of 10 in each case) resulted in copulation. There was also no evidence of asymmetry in sexual recognition. Leroy Percy male-Stoneville female pairs were just as likely to copu-

late as Stoneville male-Leroy Percy female pairs (Table 7). The number of egg sacs produced and the number of egg sacs hatching young were also similar in all Leroy Percy-Stoneville pairings. Curiously, there was some asymmetry in time to production of eggs. In the Leroy Percy-Stoneville cross, the mean time was 19.2 days; in all other crosses, the mean number of days until production of eggs was close to 12 days.

Heterotypic encounters resulted in far fewer successful matings than homotypic encounters (binomial test: 95% confidence limits for heterotypic encounters combined: 0.17, 0.44, $N = 60$, $P = 0.28$). Grenada females were far less likely to accept males than Leroy Percy or Stoneville females in all situations, and—with one exception, a successful pairing between a Grenada female and a Stoneville male—Grenada females accepted only homotypic males (Table 7). Only half of the Grenada-Grenada pairings resulted in copulation, and those that produced an egg sac subsequently produced young. The time from copulation to the production of the egg sac for pairings of Grenada females and Grenada males was nearly twice that of other pairings. In the one instance where a Grenada female accepted a heterotypic male, the time from copulation to egg sac production was near the average for pairings other than that for Grenada-Grenada pairings.

Homotypic pairings among Ohio spiders and among Leroy Percy spiders nearly always resulted in copulation (Table 8). All homotypic pairings combined resulted in nearly 85% mating success (binomial test: 95% confidence limits: 0.51, 0.97, $N = 13$, $P = 0.84$). Fewer egg sacs were produced from the Ohio pairings than from the Mississippi crosses. The Ohio-Mississippi crosses suggest that these populations are strongly, but not completely sexually isolated and that there is some asymmetry in the pattern of sexual isolation. Heterotypic pairings combined resulted in just over 50% matings (binomial test: 95% confidence limits: 0.32, 0.75, $N = 24$, $P = 0.54$). Pairings in which the female was from Ohio had a much higher rate of success than those in which the female of the pair was from the Leroy Percy population.

Table 8. Comparison of homotypic and heterotypic pairs of *Schizocosa* from populations in Ohio and Mississippi in Spring 1996

Population		No. crosses attempted	No. copulations observed	No. producing egg sac	No. egg sacs hatching eggs
Male	Female				
OH	OH	7	6	2	2
OH	MS	12	3	3	3
MS	OH	12	10	3	2
MS	MS	6	5	4	3

OH, Ohio; MS, Mississippi.

Spiders were collected 18 April (Ohio) and 24 April 1996 (Leroy Percy State Park, Mississippi) as immatures and penultimates and maintained in the laboratory.

Discussion

The results of this portion of our study indicate that although populations of *S. nr. crassipes* in the Yazoo-Mississippi Delta region of Mississippi appear to interbreed freely, nearly complete sexual isolation exists between these populations and a population from the adjacent Loess Bluff region near Grenada, Mississippi. Based on these results, we believe the Grenada population to be a distinct species although it is possible that our laboratory protocol did not include the appropriate set of environmental conditions to stimulate interbreeding. This seems unlikely, however, given our field observations of Grenada spiders which reveal a different general pattern of phenology (unpublished data). The Yazoo-Mississippi Delta populations appear to be incompletely and asymmetrically sexually isolated from a population of *S. ocreata* from Ohio, suggesting that those populations have a closer systematic affinity with *S. ocreata*.

Although the precise behavioral mechanism for the sexual isolation between the Yazoo-Mississippi Delta populations (Leroy Percy and Stoneville) and the Loess Bluff population (Grenada) is not yet known, a comparison among these populations of the frequency distributions of the four most common male displays and the sequence in which these displays are given suggest that both of these characteristics of display may be important. All three of the Yazoo-Mississippi Delta region groups (Leroy Percy I and II and Stoneville) departed significantly from a uniform frequency distribution of behaviors (Table 5, Figure 3), and with the exception of the high frequency of Arch behaviors in Stoneville males, the pattern of departure from expected was similar for all three populations: relatively more Bounce and Extension behaviors than Arch and Wave displays. In contrast, the frequency of occurrence of the male displays from Grenada showed a uniform distribution. Differences in the sequence of male display among the populations, although not as obvious as differences in the frequency distribution pattern, were evident, particularly in the pattern of facilitation of behavior, where there was no overlap in facilitating behaviors between Grenada and the two Yazoo-Mississippi Delta populations (Table 8).

CONCLUSIONS

In our survey of the geographical pattern of male courtship behavior among populations of *Schizocosa* wolf spiders in the southeastern U.S.A., we found (1) small differences in the courtship pattern of males within the same population, (2) large differences between populations in the frequency of occurrence of four male courtship displays, but no geographical pattern related to those differences, and (3) considerable homogeneity in the sequence with which male displays are given among all populations, except one from Tennessee and one from Mississippi. While we did observe interpopulation differences in the frequency of occurrence of behavior in male courtship and in the sequence of male behaviors, we do not yet know the significance of these behavioral patterns, if any, in mate selection and sexual isolation. Our study emphasizes the complexity of the courtship behavior of *S. nr. crassipes* and other members of this species group, particularly *S. ocreata*, the other brush-legged species. The potential amount of information in a typical male courtship bout is enormous and includes vibrational signals that were not included in this study. Additionally, although we observed a high level of intramale consistency in courtship display under laboratory conditions, a situation observed in other spiders (e.g., Arnqvist 1992), spider courtship is highly variable in some species. For example, the rate of bouncing in wolf spiders has been shown to be dependent on temperature (Davis 1989). Moreover, recent work by Eberhard (1994) suggests that behaviors given during copulation, so called "copulatory courtship" may be important in mating success in arthropods. The relative importance of the various components of the male courtship displays on sexual isolation in the *S. ocreata* species group has received some attention (Stratton & Uetz 1983; Hebets *et al.* 1996; Scheffer *et al.* 1996), but further studies focusing on female responses to manipulated video images are needed.

When males and females of different populations were paired experimentally, patterns of sexual isolation emerged. Two populations within the Yazoo-Mississippi Delta physiographical region appeared to inter-

breed freely, despite intrapopulation differences in the frequency of male courtship behavior in one of those populations (Leroy Percy). The population from Grenada, in the Loess Bluff physiographical region of the state, was nearly fully reproductively isolated from both of the populations in the Yazoo-Mississippi Delta. Pairings of Yazoo-Mississippi Delta populations (Leroy Percy and Stonewille) of *S. nr. crassipes* with populations of the closely related species, *S. ocreata*, from Ohio showed incomplete but strong sexual isolation. The extent to which sexual isolation is present among other populations in the region has yet to be determined. Currently, we are examining the relationships between populations on the east and west sides of the Mississippi River.

An examination of mating success and the extent of asymmetry in the sexual isolation among the groups that we compared provides some clues about the phylogenetic affinities of the populations of brush-legged spiders in the region. We conclude that the Grenada, Mississippi, population is a distinct species with closest affinities to *S. crassipes*. Phenological data from that population (G. Stratton, G. Miller & P. Miller, unpublished data) supports this conclusion. Further interpopulation pairing studies are needed to determine the relationship with this population and other populations of *S. crassipes* to the south, including the type population in Georgia. The populations in the Yazoo-Mississippi physiographical region appear to be more fully isolated from the Grenada population than from Ohio populations of *S. ocreata*. Moreover, the asymmetry of sexual isolation between the Mississippi and Ohio populations (mating success was higher when the female was from Ohio) suggests that we may have observed an intermediate stage of the divergence of traits by sexual selection (Arnold *et al.* 1996). It is likely that the southeastern *Schizocosa* *nr. crassipes* represent a species flock with an emerging pattern of species diversification.

Acknowledgments

This work was supported by grant numbers 4916-92 and 5312-94 from the National Geographic Society to G. Stratton and G. Miller, and by Hewlett Mellon Faculty Research Funds from Albion College to G. Stratton. We thank W. Miller, E. Leighton, J. Hardy, J. Latimore, and S. Ridella for help with field collections. Some specimens were obtained with support from the William H. Cross Expedition Fund of the Mississippi Entomological Museum and from NSF Grant BSR-90244810 (R. L. Brown, P.I.).

References

- Adano, S. A., & Hoy, R. R. 1994. Mating behavior of the field cricket *Gryllus bimaculatus* and its dependence on social and environmental cues. *Animal Behaviour*, **47**, 857–868.
- Aspey, W. P. 1977. Wolf spider sociobiology. I. Agonistic display and dominance-subordinance relations in adult male *Schizocosa crassipes*. *Behaviour*, **62**, 103–141.
- Arnold, S. J., Verrell, P. A., & Tilley, S. G. 1996. The evolution of asymmetry in sexual isolation: a model and a test case. *Evolution*, **50**, 1024–1033.
- Arnqvist, G. 1992. Courtship behavior and sexual cannibalism in the semi-aquatic fishing spider *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae). *Journal of Arachnology*, **20**, 222–226.
- Bush, G. L. 1992. Host race formation and sympatric speciation in *Rhagoletis* fruit flies (Diptera: Tephritidae). *Psyche*, **99**, 335–353.
- Bush, G. L. 1994. Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology and Evolution*, **9**, 285–288.
- Clark, D. L. 1994. Sequence analysis of courtship behavior in the dimorphic jumping spider *Maevia inclemens* (Araneae, Salticidae). *Journal of Arachnology*, **22**, 94–107.
- Coyne, J. A. 1989. Genetics of sexual isolation between two sibling species. *Drosophila simulans* and *Drosophila mauritiana*. *Proceedings of the National Academy of Sciences U.S.A.*, **86**, 5464–5468.
- Coyne, J. A. 1993. The genetics of an isolating mechanism between two sibling species of *Drosophila*. *Evolution*, **47**, 778–788.
- Davis, D. L. 1989. The effect of temperature on the courtship behavior of the wolf spider *Schizocosa roveri* (Araneae: Lycosidae). *American Midland Naturalist*, **122**, 281–287.
- Dingle, H. 1969. A statistical and information analysis of aggressive communication in the mantis shrimp, *Conodactylus brendini* Manning. *Animal Behaviour*, **17**, 561–575.
- Dobzhansky, T. 1970. *Genetics of the Evolutionary Process*. New York: Columbia University Press.
- Dondale, C. D. & Redner, J. H. 1978. Revision of the nearctic wolf spider genus *Schizocosa* (Araneida: Lycosidae). *Canadian Entomologist*, **110**, 143–181.
- Eberhard, W. G. 1994. Evidence for widespread courtship during copulation in 121 species of insects and spiders, and implications for cryptic female choice. *Evolution*, **48**, 711–733.
- Eberhard, W. G. 1985. *Sexual Selection and Animal Genitalia*. Cambridge, Massachusetts: Harvard University Press.
- Eherman, L., & Wasserman, M. 1987. The significance of asymmetrical sexual isolation. *Evolutionary Biology*, **21**, 1–20.
- Feder, J. L., Opp, S. B., Wlazlo, K., Go, W., & Spisak, S. 1994. Host fidelity is an effective premating barrier between sympatric races of apple maggot fly. *Proceedings of the National Academy of Sciences of the U.S.A.*, **91**, 7990–7994.
- Futuyma, D. J., & Mayer, G. C. 1980. Non-allopatric speciation in animals. *Systematic Zoology*, **29**, 254–271.
- Hebets, E. A., Stratton, G. E., & Miller, G. L. 1996. Habitat and courtship behavior of the wolf spider *Schizocosa retrorsa* (Banks) (Araneae; Lycosidae). *Journal of Arachnology*, **24**, 141–147.
- Henry, C. S. 1983. Acoustic recognition of sibling species within the holarctic lacewing *Chrysoperia cornea* (Neuroptera: Chrysopidae). *Systematic Entomology*, **8**, 293–301.
- Henry, C. S., Wells, M. M., & Pupedis, R. J. 1993. Hidden taxonomic diversity within *Chrysoperia plorabunda* (Neuroptera: Chrysopidae): two new species based on courtship songs. *Annals of the Entomological Society of America*, **86**, 1–13.
- Houck, L. D., Arnold, S. J., & Hickman, A. 1988. Tests for sexual isolation in plethodontid salamanders (genus *Desmognathus*). *Journal of Herpetology*, **22**, 186–191.
- Johnson, P. A., Hoppensteadt, F. C., Smith, J. J., & Bush, G. L. 1996. Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. *Evolutionary Ecology*, **10**, 187–205.
- Kaneshiro, K. 1976. Ethological isolation and phylogeny in the planitibia subgroup of Hawaiian *Drosophila*. *Evolution*, **30**, 740–745.

- Koepfer, H. R. 1987. Selection for sexual isolation between geographic forms of *Drosophila mojavensis*. II. Effects of selection of mating preference and propensity. *Evolution*, **41**, 1409–1413.
- Krebs, R. A. & Markow, T. A. 1989. Courtship behavior and control of reproductive isolation in *Drosophila mojavensis*. *Evolution*, **43**, 908–913.
- Markow, T. A. 1981. Courtship behavior and control of reproductive isolation between *Drosophila mojavensis* and *Drosophila arizonensis*. *Evolution*, **35**, 1022–1026.
- Markow, T. A., & Hanson, S. J. 1981. Multivariate analysis of *Drosophila* courtship. *Proceedings of the National Academy of Sciences U.S.A.*, **84**, 430–434.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, Massachusetts: Harvard University Press.
- Moodie, G. E. E. 1982. Why asymmetric mating preference may not show the direction of evolution. *Evolution*, **36**, 1096–1097.
- Rice, W. R., & Salt, G. W. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution*, **44**, 1140–1152.
- Ringo, J. M., Wood, D., Rockwell, R., & Dowse, H. 1985. An experiment testing two hypotheses of speciation. *American Naturalist*, **126**, 642–661.
- Scheffer, S. J., Uetz, G. W., & Stratton, G. E. 1996. Sexual selection, male morphology, and the efficacy of courtship signaling in two wolf spiders (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology*, **38**, 17–24.
- Schliwien, U. K., Tautz, D., & Paeaebo, S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature*, **368**, 629–632.
- Schmidt, G. 1990. Courtship behaviour, copulation and crossing experiments in *Latrodectus* species (Araneida: Theridiidae). *Acta zoologica fennica*, **190**, 351–355.
- Sokal, R. R., & Rohlf, F. J. 1995. *Biometry*. 3rd edn. New York: W. H. Freeman.
- Speith, H. T. & Ringo, J. M. 1983. Mating behaviour and sexual isolation in *Drosophila*. In: *The Genetics and Biology of Drosophila* (Ed. by M. Ashburner, H. L. Carson & J. N. Thompson, Jr.), pp. 223–284. New York: Academic Press.
- Stratton, G. E. 1991. A new species of wolf spider, *Schizocosa stridulans* (Araneae: Lycosidae). *Journal of Arachnology*, **19**, 29–39.
- Stratton, G. E. 1997a. A new species of *Schizocosa* from the Southeastern USA (Araneae, Lycosidae). *Journal of Arachnology*, **25**, 84–92.
- Stratton, G. E. 1997b. Investigation of species divergence and reproductive isolation of *Schizocosa stridulans* (Araneae: Lycosidae) from Illinois. *Bulletin of the British Arachnological Society*, **10**, 313–321.
- Stratton, G. E., & Lowrie, D. C. 1984. Courtship behavior and life cycle of the wolf spider *Schizocosa mccoeki* (Araneae: Lycosidae). *Journal of Arachnology*, **12**, 223–228.
- Stratton, G. E., & Uetz, G. W. 1981. Acoustic communication and reproductive isolation in two species of wolf spider. *Science*, **214**, 575–577.
- Stratton, G. E., & Uetz, G. W. 1983. Communication via substratum-coupled stridulation and reproductive isolation in wolf spiders (Araneae: Lycosidae). *Animal Behaviour*, **31**, 164–172.
- Stratton, G. E., & Uetz, G. W. 1986. The inheritance of courtship behavior and its role as a reproductive isolating mechanism in two species of *Schizocosa* wolf spiders (Araneae: Lycosidae). *Evolution*, **40**, 129–141.
- Stratton, G. E., Hebets, E. A., Miller, P. R., & Miller, G. L. 1996. Pattern and duration of copulation in wolf spiders (Araneae, Lycosidae). *Journal of Arachnology*, **24**, 186–200.
- Tanaka, H., & Suwa, M. 1986. Descriptions of three new spiders of the *Pardosa laura* complex (Araneae: Lycosidae) based on their morphology and ecology. *Acta Arachnologica*, **34**, 49–60.
- Tauber, C. A. 1977a. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature*, **268**, 702–705.
- Tauber, C. A., & Tauber, M. J. 1977b. Sympatric speciation based on allelic changes at three loci: evidence for natural populations in two habitats. *Science*, **197**, 1298–1300.
- Uetz, G. W., & Denterlein, G. J. 1979. Courtship behavior, habitat, and reproductive isolation in *Schizocosa royneri* Uetz & Dondale (Araneae: Lycosidae). *Journal of Arachnology*, **7**, 86–88.
- Uetz, G. W., & Dondale, C. D. 1979. A new wolf spider in the genus *Schizocosa* (Araneae: Lycosidae) from Illinois. *Journal of Arachnology*, **7**, 86–88.
- Uetz, G. W., & Stratton, G. E. 1982. Acoustic communication and reproductive isolation in spiders. In: *Spider Communication: Mechanisms and Ecological Significance* (Ed. by P. N. Witt & J. S. Rovner), pp. 123–159. Princeton, New Jersey: Princeton University Press.
- Uetz, G. W., McClintock, W., Miller, D., Smith, E. L., & Cook, K. K. 1996. Limb regeneration and subsequent asymmetry in a male secondary sexual character influences sexual selection in wolf spiders. *Behavioral Ecology and Sociobiology*, **38**, 253–257.
- Verrell, P. A. 1989. An experimental study of the behavioral basis of sexual isolation between two sympatric plethodontid salamanders, *Desmognathus imitator* and *D. ochrophaeus*. *Ethology*, **80**, 274–282.
- Verrell, P. A., & Arnold, S. J. 1989. Behavioral observations of sexual isolation among allopatric populations of the mountain dusky salamander, *Desmognathus ochrophaeus*. *Evolution*, **43**, 745–755.
- Watanabe, T. K., & Kawanishi, M. 1979. Mating preference and the direction of evolution in *Drosophila*. *Science*, **205**, 906–907.
- Wasserman, M., & Koepfer, H. R. 1977. Character displacement for sexual isolation between *Drosophila mojavensis* and *Drosophila arizonensis*. *Evolution*, **31**, 812–823.
- Wasserman, M., & Koepfer, H. R. 1980. Does asymmetrical mating preference show the direction of evolution? *Evolution*, **34**, 1116–1126.
- Welbergen, P., Van Dijken, F. R., & Scharloo, W. 1987. Collation of the courtship behaviour of the sympatric species *Drosophila melanogaster* and *Drosophila simulans*. *Behaviour*, **101**, 253–274.
- Wise, D. H., & Wagner, J. D. 1992. Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. *Oecologia*, **91**, 7–13.