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COURTSHIP BEHAVIOR, HABITAT, AND REPRODUCTIVE ISOLATION IN *SCHIZOCOSA ROVNERI* UETZ AND DONDALE (ARANEAE: LYCOSIDAE)

George W. Uetz and Geraldine Denterlein

Department of Biological Sciences
University of Cincinnati, Cincinnati, Ohio 45221

ABSTRACT

The courtship behavior of *Schizocosa rovneri* Uetz and Dondale is described and analyzed. Courtship behavior in this species is distinct from that of *Schizocosa ocreata* (Hentz), although these species are morphologically very similar and indistinguishable on the basis of genitalia.

Males of both species courted conspecific and heterospecific females with almost equal frequency. However, females only responded receptively and copulated with conspecific males. Males of *S. rovneri* exhibited quantitative differences in aspects of courtship behavior in response to different stimuli. In the presence of a conspecific female, the searching phase was shorter and less variable, and the stridulation bouts were three times as frequent than with heterospecific females. Values of these parameters for male *S. rovneri* with only the silk (and pheromone) of a conspecific female were intermediate.

Data on habitat and seasonal occurrence of the two species suggest that *S. ocreata* breeds earlier in the season and prefers upland forest areas, while *S. rovneri* breeds 2-3 weeks later and prefers bottomland forest and river flood plains. It is suggested that differences in courtship behavior serve to maintain reproductive isolation in these two species, whose spatial and temporal isolation is incomplete.

INTRODUCTION

A wide variety of animals have been studied with respect to reproductive behavior, and it is suggested that in many the sequences of behaviors leading to copulation functions to ensure reproductive isolation (Crane 1955; Jacobs 1955; Stride 1956, 1958). Hybrids between populations are frequently less fit than either parent. When this occurs, selection acts to prevent reproductive "mistakes" (Bush 1975). Individuals possessing characteristics which emphasize differences between populations (courtship and mating factors) will contribute more offspring to future generations (White 1978).

It is possible that a variety of arthropod populations that rarely interbreed in nature are capable of doing so, but owing to seasonal and habitat differences, and possibly reproductive behavior, do not actually interbreed. A species reproductively isolated from other groups by behavioral mechanisms occuring in courtship is known as an "ethospecies" (Hollander and Dijkstra 1974). This definition becomes useful when morphological characteristics are indistinct between groups or show a large gradation (Hollander et al. 1973).

Arthropod systematists have traditionally relied heavily on morphological characteristics of genitalia in determining species, but are the first to admit to the limitations of the method. The logic behind the system is sound enough - morphological differences in genitalia serve to maintain reproductive isolation in a "lock-and-key" fashion (Gering 1953). This line of reasoning cannot explain cases of identical genitalia that do not interbreed. These species are known as "cryptic" species, as they often go undetected (Walker 1964). Studies of calling songs and reproductive communication in crickets and longhorned grasshoppers have revealed numerous species that were unrecognized on the basis of morphological studies (Walker 1957). It is estimated that a sizeable number of species in a variety of animal taxa are cryptic by commonly used taxonomic standards, yet are reproductively isolated and thus are valid species just the same.

Clarification of taxonomic problems with interbreeding experiments and behavioral studies has been attempted with spiders with a high degree of success (Taylor and Peck 1975; Dondale 1964, 1967; Rovner 1973). Hollander et al. (1973) examined reproductive barriers in *Pardosa* (Araneae: Lycosidae), and found habitat, seasonality and courtship behavior to be of great importance in clarifying species relationships. Hollander and Dijkstra (1974) discovered an ethospecies, *Pardosa vlijmi*, separated from a sibling species by courtship behavior alone.

This paper concerns behavioral clarification of species identity in the recently revised North American spider genus *Schizocosa* (Araneae: Lycosidae) (Dondale and Redner 1978). *Schizocosa ocreata* (Hentz) is a wolf spider common in deciduous forest litter in eastern North America. *Schizocosa rovneri*, Uetz and Dondale, from Illinois is apparently identical to *S. ocreata* with respect to genital characters, body size, general morphology, color, etc. It does, however, lack the prominent (although variable) tufts of black bristles on the tibiae of leg I present on males of *S. ocreata*. The courtship and mating behavior of these two species is clearly different; and females will copulate only with conspecific males. It is probable that *S. rovneri* is a valid ethospecies, reproductively isolated from *S. ocreata* by courtship behavior.

METHODS

During the course of doctoral research at the University of Illinois (1972-1976), one of us (GU) collected large numbers of specimens of *Schizocosa* wolf spiders. These specimens were identified as *S. ocreata* (at that time called *S. crassipes*) on examination of genital characters. However, males lacked the characteristic tufts of dense black bristles on the tibia of leg I. Similar specimens had been reported in Delaware (Uetz 1977), in Arkansas (Peck and Whitcomb, in press), and North Carolina (Berry 1971). Our original intent was to determine if internal parasites were suppressing development of the tibial brushes in individuals from Illinois. The brushes are a secondary sexual characteristic and would be likely to be lacking in cases of parasitic castration. Finding no parasites, we attempted to crossmate individuals from brushless and typical populations to see if they were reproductively compatible.

Individuals of the suspected new species, *S. rovneri*, were collected as immatures in the antepenultimate instar in March 1977, in the flood plain of Hart Memorial Woods, located on the Sangamon River near Mahomet, Illinois. Field data on phenology and habitat were available from a pitfall trap study on the Sangamon River nearby (Uetz 1976). In May 1977, immature *S. ocreata* in the penultimate instar were collected at Strouds Run State Forest near Athens, Ohio. Specimens were housed separately in in-

Table 1.–Behavioral responses of male and female *Schizocosa* to the presence of other individuals or their silk (and pheromones). (+) indicates a positive response (courtship if the specimen is a male; receptivity if the specimen is a female), while (–) indicates no response or a negative response (avoidance or agonistic behavior).

	S. ocreata (Ohio)		*S. rovneri* (Illinois)	
MALES	+	–	+	–
with conspecific female	8	1	11	1
with conspecific female silk (and pheromone)	10	0	10	0
with heterospecific female	9	1	8	0
with heterospecific female silk (and pheromone)	10	0	10	0
FEMALES				
with conspecific male	6	3	11	1
with heterospecific male	0	8	0	10

dividual, clear plastic, rectangular containers (7cm x 7cm x 13cm). Each container had a cotton-plugged vial filled with water, which provided a source of moisture. Each spider was fed a mealworm (*Tenebrio molitor* L.) every 3-5 days. All spiders were placed in a growth chamber in order to insure a natural day/night temperature and light cycle (23°C day, 13°C night; with 13 hours light; 11 hours dark) and prolong the life of the specimens.

Mating experiments for this study took place in late May and early June 1977. Tests were conducted in a circular culture dish (19cm diam; 7cm depth) with a piece of white bond paper covering the floor of the container. Females of either species were placed in the container and allowed to move freely for 3-5 hours. They were removed and a conspecific or heterospecific male was placed in the container and observed for 20 min. for evidence of courtship response to the silk and/or pheromone present in the silk. Courtship behavior of males with a female present was observed by placing a plastic divider in the culture dish, separating the male and female. Conspecific and heterospecific pairs were observed for twenty minutes, and evidence of female receptivity was noted. Courtship behavior was recorded on film and descriptive accounts of the behavior were whispered into a tape recorder while observing the specimens. A stop watch was used to record the time intervals between stridulation and the time of searching behavior. In some cases individuals were allowed to come in contact with each other (without the divider).

RESULTS

Courtship behavior was displayed by males of *Schizocosa rovneri* and *S. ocreata* in most test cases (Table 1). Males of both groups courted conspecific and heterospecific females with almost equal frequency. However, females only responded receptively in the presence of a conspecific male.

The behavior of receptive female *S. rovneri* closely resembled that of *S. saltatrix* (Rovner 1974). The female lowered her cephalothorax and extended her forelegs on the substrate, then rose, turned 90°-180° in the opposite direction and repeated the procedure. Several turns were executed in rapid succession, followed by mounting by the male

Table 2.–Comparison of courtship behavior of *Schizocosa* males.

Behavioral Phase	*S. ocreata* (Ohio)	*S. rovneri* (Illinois)
Searching	distinct in-unison raising of first pair of legs, tapping on substrate; palpal movements–stridulation	legs extended, probing in random fashion, palpal movements without stridulation (palps scraped on substrate, then alternately raised and moved past chelicerae)
Display	forelegs alternately raised, arched, and extended forward	forelegs extended in contact with substrate; spine erection over entire body; body raised, then lowered rapidly and bounced on substrate; impact of bounce produces abdominal reverberations
Stridulation	barely audible; accompanies leg tapping	audible; producing a "buzzing" sound; occurs in short bursts accompanying "bounce"

(when the divider was removed). Female *S. rovneri* exhibited this sequence of behaviors in the presence of conspecific males in 11 out of 12 trials, but never in the presence of heterospecific males.

Several conspecific matings were allowed for each group by removing the divider. Copulation was characteristic for the genus, as described by Rovner (1973), and resulted in offspring in all cases. Heterospecific pairings without the divider never resulted in copulation despite numerous attempts by males to mount. Females in these cases responded to males with avoidance or agonistic behavior.

The courtship behavior of *Schizocosa rovneri* differed in many respects from that of *S. ocreata* (Table 2). The courtship sequence began with a searching phase, which consisted of raising, extending and lowering the forelegs in a probing fashion. A series of rapid palpal scraping movements occurred during searching, followed by alternately raising the palps to the chelicerae. Tietjen (pers. comm.) has suggested that these behaviors are associated with the cleaning of silk from pedipalps and not with olfaction. After a variable number of palpal scraping movements, the male entered a stationary phase wherein the legs with extended and the palps were held perpendicular to and in contact with the substrate. The display phase which followed consisted of several bouts of stridulation (produced by the stridulatory organs in the male palp (Rovner 1975), which produced a clearly audible sound characterized as a "buzz". This was followed by a brief period of inactivity, after which the spider would either go through another entire courtship sequence beginning at the searching phase, or change position and resume stridulation.

Analysis of high speed films (58 fps) of courtship in *S. rovneri* males has revealed a unique movement of the entire body associated with stridulation. The spider first raised the cephalothorax and abdomen slightly, then thrust the body downward between the legs, hitting the substrate with a "bounce". Rotating movements of the palps were observed at this point, indicating stridulation. Reverberation of the bounce impact was noted in the entire body, and was particularly visible in the abdomen, which continued to vibrate for a few fractions of a second. The onset of stridulation and reverberation of the

Table 3.–Quantitative analysis (means indicated with ± 1 S.E.) of behavior exhibited by *S. rovneri* males during courtship. (*=only two measurements available; **=means are significantly different [T-test; $p<0.01$]).

	N	No. exhibiting courtship	$\bar{x}$ time in searching mode (sec)	$\bar{x}$ stridulation frequency (no./10 sec)	$\bar{x}$ interval between bouts of stridulation**
with conspecific female	10	9	30.44±2.89	2.06±.17	12.23± 3.28
with conspecific silk (and pheromone)	10	10	61.80±19.26	2.39±.35	28.04± 4.53
with heterospecific female	5	5	48.20±11.05	1.65±.35	35.0±85.0*
with heterospecific silk (and pheromone)	10	10	46.78±14.86	2.35±.21	63.48±18.53

bounce impact were simultaneous and appear (when viewed at normal speed) as a "jerk" or "spasm".

Although males of *S. rovneri* and *S. ocreata* displayed to conspecific and heterospecific females and in response to their silk, there is evidence that male *S. rovneri* exhibit quantitative differences in courtship behavior in response to different stimuli (Table 3). There was a significant decrease in the variability of searching time when males were placed with conspecific females, as compared with all other trials, although mean search time was not significantly different. The time interval between bouts of stridulation was significantly decreased ($p<0.01$) in the presence of conspecific females and their silk vs. heterospecific females or their silk. Also, interval time was significantly lower in the presence of conspecific females vs. pheromone alone ($p<0.01$).

DISCUSSION

Observations made in the laboratory of *S. ocreata* and the new species *S. rovneri* clearly indicate that there is a significant difference in courtship behavior of the two groups. This is important in light of the fact that the two groups are morphologically identical with respect to genital characteristics. The only apparent morphological difference between the groups is that male *S. ocreata* have a dense brush of black setae on the tibia of leg I which is absent in *S. rovneri*. It is possible that the brush is important in the courtship behavior of *S. ocreata*, which includes raising, extension and tapping of the first pair of legs. The brush might provide an important visual cue for the female. *S. rovneri* seems to rely less on the visual aspects of courtship; but rather, relies heavily on the auditory effect of vibrations created by the stridulatory organs on the male palp.

Behavioral differences were not only noted between *S. ocreata* and *S. rovneri* but also within the response of *S. rovneri* to conspecific and heterospecific females and their silk. Silk of adult female wolf spiders has been shown to contain a sex peromone which elicits the courtship response of male spiders (Rovner 1968). Male *S. rovneri* displayed courtship in almost all trial cases. However, in the presence of a conspecific female, the searching phase was shorter and less variable, and the stridulation bouts more frequent. Without a plastic barrier, copulation occurred within two minutes in most cases. In cases of male *S. rovneri* with heterospecific female or silk of either species, the searching phase was longer

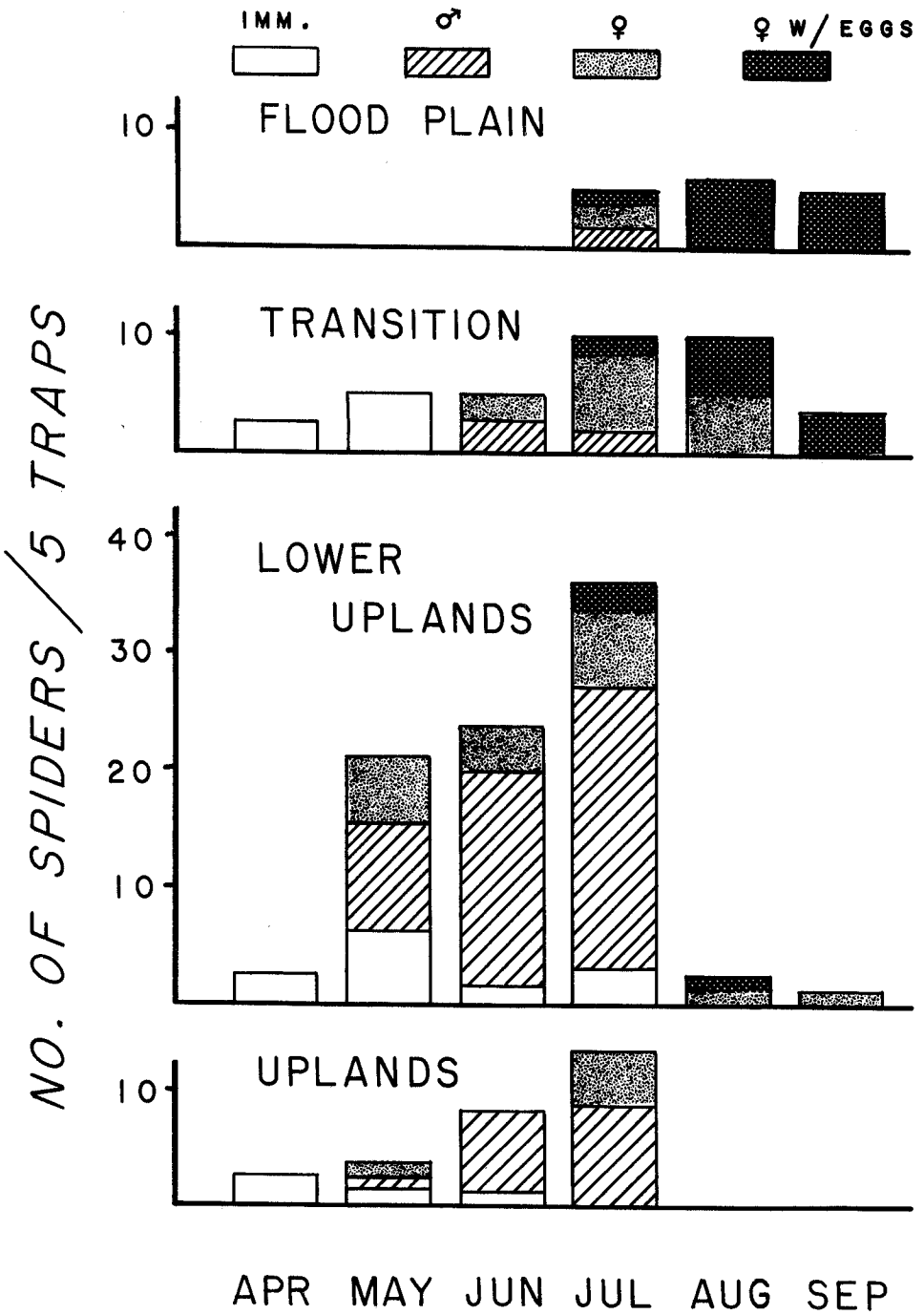

Fig. 1.–Seasonal abundance of *Schizocosa rovneri* at four elevations on a flooding gradient. The site is the streamside forest at Robert Allerton Park, on the Sangamon River in central Illinois.

and more variable and courtship was not as vigorous in terms of frequency of stridulation bouts. This suggests that the male *S. rovneri* court conspecific females more readily and more efficiently in response to some recognition factor.

It appears that the female response is ultimately the critical factor in the isolation of these two species. While males of each species court females of both species, the females only respond to and copulate with members of their own species. Female *S. rovneri* respond almost immediately to the stridulation of male *S. rovneri* but not to the palpal tapping of *S. ocreata*. It is clear that sexual communication through stridulation plays a major role in the reproductive isolation of these species.

Our collections of *Schizocosa rovneri* (as well as collections mentioned in the literature we suspect are *S. rovneri*–Berry 1971; Uetz 1977; Peck and Whitcomb, 1978) are well within the geographic range of *S. ocreata*. Interestingly, the microhabitat preferences and seasonal occurrence of all four populations of suspected *S. rovneri* were similar to each other, yet distinct from *S. ocreata* populations. *Schizocosa ocreata* is common in Illinois, and has even been taken in the same study area where we collected *S. rovneri*. Data on habitat and seasonal occurrence are available on both species, and suggest that *S. ocreata* breeds earlier in the season and prefers upland forest areas. *S. rovneri* breeds later and prefers bottomland forest habitat and river flood plains. It is a species in which habitat, seasonality and behavior interact in reproductively isolating the species from others. Pitfall trap collections of *S. rovneri* at different elevations in an Illinois flood plain forest over the breeding season show the influence of vernal flooding on the temporal and spatial occurrence of the new species (Figure 1). We might hypothesize that populations of *Schizocosa* occuring in low-lying areas have a later season of breeding than populations in higher areas, and are phenologically "out of phase" with upland populations.

Differences in courtship behavior would appear to be important in maintaining the reproductive isolation of the two groups (since they are not completely isolated by habitat or season), and thus are crucial in maintaining species' genetic integrity. For this reason, we feel *Schizocosa rovneri* is a valid "etho-species". Further research is currently underway to determine interfertility of populations, and to examine geographic variability in behavior. New information will aid our understanding of the problematical taxonomy of the Lycosidae.

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