

# The Great Lakes Entomologist

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Volume 25  
Number 4 - Winter 1992 *Number 4 - Winter*  
1992

Article 7

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October 1992

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### Recommended Citation

Drickamer, Lee C. and McPherson, J. E. 1992. "Comparative Aspects of Mating Behavior Patterns in Six Species of Stink Bugs (Heteroptera: Pentatomidae)," *The Great Lakes Entomologist*, vol 25 (4)  
Available at: <https://scholar.valpo.edu/tgle/vol25/iss4/7>

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## COMPARATIVE ASPECTS OF MATING BEHAVIOR PATTERNS IN SIX SPECIES OF STINK BUGS (HETEROPTERA: PENTATOMIDAE)

Lee C. Drickamer<sup>1</sup> and J. E. McPherson<sup>1</sup>

## ABSTRACT

Mating sequences were analyzed for six species of stink bugs using videotapes. The results consisted of qualitative descriptions of the precopulatory activities of the pairs and quantitative analyses of the number and direction of mating sequences, including the latency to and duration of copulatory lock. It was possible to quantitatively characterize each of the six species tested. In addition, certain infrequent behavior patterns, e.g., head butts, were observed for some species and not others. The results extend the previous information on mating activities in stink bugs, particularly for *Euschistus*. We interpret our findings with regard to reproductive strategies in different species of stink bugs, and consider the use of behavior as a taxonomic tool.

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Locating mates and mating behavior are critical aspects of insect behavioral biology; these issues have been emphasized, both in general theoretical terms and studied in particular species (Matthews and Matthews 1978, Thornhill and Alcock 1983). Sexual behavior patterns have been investigated in several North American species. Descriptions of all or portions of mating sequences are available for *Murgantia histrionica* (Hahn) (Lanigan and Barrows 1977), *Cosmopepla bimaculata* (Thomas) (Fish and Alcock 1973, Olsen 1910), *Nezara viridula* (L.) (Harris and Todd 1980, Mitchell and Mau 1969), *Brochymena sulcata* Van Duzee (Ruckes 1938), *B. quadripustulata* (Fabricius) (Gamboa and Alcock 1973), and *Euschistus conspersus* Uhler (Alcock 1971). Attractant pheromones have been identified in some species (Aldrich 1988) and it has been hypothesized that, at least in *N. viridula*, the pheromone operates over a relatively long distance followed by touching behavior (Harris et al. 1982). Furthermore, in *N. viridula*, a sophisticated auditory communication system may act as an intermediate step between the pheromone and touch mode (Harris et al. 1982). In all of the species tested, a precopulatory mating sequence is carried out while the members of the prospective pair are in close proximity to one another.

Although stink bugs share elements of their mating activities, inter- and intraspecific variation exist in courtship. The most frequent elements include males using their antennae to palpate various parts of the female; making head contact with the female, involving simple touching contact, head butts and attempts to lift the rear of the female abdomen; and the male turning so that the partners face in opposite directions (the end-to-end copulatory position; Gamboa and Alcock 1973). Several reports concern the pattern of the sequence as the male palpates and makes contact with the female (Alcock

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1971, Gamboa and Alcock 1973, Lanigan and Barrows 1977), the latency to copulatory linkage (Alcock 1971, Harris and Todd 1980, Lanigan and Barrows 1977), and the duration of the linkage (Fish and Alcock 1973, Harris and Todd 1980, Lanigan and Barrows 1977, Tostowaryk 1971).

Some elements of the mating and copulatory sequence could be important cues for species recognition and other elements may be related to species-specific mating strategies. The major purpose of this paper is to describe the mating sequences for six sympatric species of stink bugs from southern Illinois, five from the same genus. Our results suggest that differences in courtship patterns could serve as aids for species recognition, and add to existing information on mating sequences in stink bugs.

Our findings also are relevant to the potential use of behavior as a taxonomic tool as has been attempted previously for various mammals (Bekoff et al. 1975, Dewsbury 1972), and the bird orders Pelicaniformes (Van Tets 1965) and Anseriformes (Lorenz 1972), as well as for several insects (e.g. wasps [Evans 1966] and ants [Wilson 1971]). The possible benefits from a cross-fertilization between ethology and phylogenetic systematics are apparent from recent work on fish (McLennan et al. 1988).

## MATERIALS AND METHODS

We observed six species of stink bugs: *Euschistus ictericus* (L.), *E. politus* Uhler, *E. servus* (Say), *E. tristigmus* (Say), *E. variolarius* (Palisot de Beauvois), and *Thyanta custator accerra* McAtee. All were reared under laboratory conditions from wild stocks taken from the La Rue - Pine Hills Ecological Area of the Shawnee National Forest, southern Illinois. The various stocks were reared according to the procedures developed by McPherson and Mohlenbrock (1976). Field-collected parents were kept in Mason jars in incubators maintained at  $23 \pm 1^\circ\text{C}$  and a 16L:8D photoperiod. Each jar contained a circular piece of filter paper covering the bottom, and beans or carrots served as food. Strips of paper towel were added to each jar to increase the area for footing and excrement absorption. Several 3 cm x 5 cm strips of cheesecloth were placed in each jar to serve as oviposition sites. Each jar was closed with a screen mesh top, a disc of paper toweling, and the ring of the two-piece jar lid.

Cheesecloth with attached egg clusters was removed and placed in Petri dishes on moist filter paper and maintained under the same ambient conditions as the parents. First instars (a nonfeeding stage) were maintained in the same Petri dishes. Second through fifth instars were reared in Mason jars in a fashion similar to that described for maintaining adults. Upon reaching adults, the bugs were separated by sex and maintained in separate Mason jars until used in mating tests. We tested the mating sequences of the stink bugs about two weeks after they emerged as adults because previous observations (unpublished data) indicated they are prepared to mate by two weeks after the final molt.

We used a Panasonic Digital 5000 camera system with a zoom lens and a Panasonic AG-6010s VHS tape deck to videotape mating activities of stink bugs. Playback was done on a Sony 40 cm color monitor. The tape deck permitted us to view tapes in slow motion or to stop the tape to make a record of the time. The camera system was equipped with a continuous timer display, reading to the nearest second.

The videotaping session involved placing either 2 males and 2 females or 3 males and 3 females of a designated species into a 250 ml beaker (5 cm in diam, 7.5 cm deep) closed with a Petri dish lid. Each beaker contained a piece of cheesecloth taped to the rear wall as seen on the television monitor and, in

many instances, several beans were added to the bottom of the container. Two observation chambers were placed side-by-side and filmed simultaneously. Most stink bug activity occurred on either the cheesecloth or the beans. In a few instances ( $n < 5$  cases for all species combined), the bugs' locations made it impossible to accurately record the mating and copulatory sequence completely. In these instances, we discarded the data from our sample.

Animals were placed into the observation chambers for approximately 24 hours. A standard 2-hour videotape cassette was used with the machine set to record every 12th frame, thus permitting us to tape 24 hours of activity with a single tape. Preliminary data from the tapes indicated that recording every 12th frame was sufficient to obtain an accurate record of the behavior sequences.

Based on preliminary observations of videotapes, we recorded the following dependent variables associated with mating activities and copulation: (1) number of mating sequences, defined as a series of antennal palpations of the female by the male, followed by or in conjunction with head contact by the male to the thorax, abdomen and rear of the female, culminating in an attempt by the male to turn around and achieve intromission; (2) the orientation of the male with respect to the female during courtship, with the male initiating contact with the female's head (or tip of abdomen) and moving to the tip of her abdomen (or head); (3) latency from initial contact via antennation until intromission was achieved; and (4) duration of copulation. In addition, we noted behavior patterns for each species. Our results consist of quantitative observations that we have analyzed statistically, using Chi-square and ANOVA (Sokal and Rohlf, 1983), and qualitative descriptions of behavior patterns for each species.

## RESULTS

Analysis of the videotapes provided an opportunity to describe the mating sequences for the six species. After initial contact between members of a pair, the general pattern involved a series of antennal palpations of the female by the male; antennal contact occurred with the head, thorax and abdomen of the female, and varied according to species. The direction of palpation of the female's body from either head to abdomen or abdomen to head also varied. Antennal palpation was followed by, or occurred in conjunction with, head contact by the male with some or all of the three body regions of the female; here also the direction of the sequence of contacts was from head to rear or vice versa. The final stages of the sequence involved the male turning his body  $180^\circ$  so that the rear of his abdomen was in contact with the rear of her abdomen in the pattern characteristic of the Pentatomoidea; at this point the male attempted intromission. Differences occurred among species in the number of times the male completed the entire sequence from palpation to attempted intromission. In addition, there were other species differences in the courtship sequence, including head butts of the female by the male, and variations when the male turned around to assume the end-to-end copulatory position. In the latter instance, some males completed the turn with their body remaining in contact with the female, sliding the rear of their body along the thorax and abdomen of the female until genital-to-genital contact occurred while for other males, there was little or no contact between the partners.

Quantitative analyses, using Chi-square contingency tests as the basis for generating expected values, revealed significant differences among species for both the number of mating sequences that occurred before copulation ( $X^2 = 25.52$ ; d.f. = 5;  $p < 0.001$ ; Table 1) and the direction of the sequence ( $X^2 =$

Table 1. — Numbers (A) of mating and copulation sequences and (B) direction of the mating sequence for pairs of stink bugs of six species.<sup>a</sup>

Species (sample size = # pairs)	Number of Pairs Exhibiting 1 or 2+ Mating Sequences Before Copulation	
	1	2+
<i>Euschistus ictericus</i> (11)	3 (5.6)	8 (4.5)
<i>Euschistus politus</i> (16)	16 (9.4)	0 (6.6)
<i>Euschistus servus</i> (11)	9 (6.5)	2 (4.5)
<i>Euschistus tristigmus</i> (19)	4 (11.2)	15 (7.8)
<i>Euschistus variolarius</i> (14)	9 (8.2)	5 (5.8)
<i>Thyanta custator accerra</i> (9)	6 (5.3)	3 (3.7)

  

Species (sample size = # pairs)	Direction of Mating Sequence	
	Head-to-rear	Rear-to-head
<i>Euschistus ictericus</i> (11)	10 (8.5)	1 (2.5)
<i>Euschistus politus</i> (16)	16 (12.4)	0 (3.6)
<i>Euschistus servus</i> (11)	11 (8.5)	0 (2.5)
<i>Euschistus tristigmus</i> (19)	11 (14.7)	8 (4.3)
<i>Euschistus variolarius</i> (14)	13 (10.8)	1 (3.2)
<i>Thyanta custator accerra</i> (9)	1 (7.0)	8 (2.0)

<sup>a</sup>For each dependent measure, the expected values from a contingency Chi-square test are given in parentheses.

30.06; d.f. = 5;  $p < 0.001$ ; Table 1). For number of mating sequences, there were two significant deviations from the expected values; *E. politus* exhibited more single sequences than expected and *E. tristigmus* exhibited two or more sequences more frequently than expected. In *E. politus*, the observed value for sequences going from head to rear during palpation and head contact was greater than expected. Also, for both *E. tristigmus* and *T. c. accerra*, the observed frequencies for sequences going from the rear to the head were greater than expected.

Latencies to copulatory linkage varied significantly across the six species ( $F = 9.85$ ; d.f. = 5,74;  $p < 0.001$ ; Table 2). *E. politus*, *E. variolarius*, and *T. c. accerra*, which did not differ from each other in latency to copulation, all achieved linkage more rapidly than the other three species; the latter three also did not differ from one another. There were also significant differences in the duration of the copulatory linkage ( $F = 8.88$ ; d.f. = 5,74;  $p < 0.001$ ; Table

Table 2. — Latency (sec) to establishment of copulatory linkage and duration (min) of the copulatory linkage in six species of stink bugs.<sup>a</sup>

Species (sample size = # pairs)	Latency (sec)	Duration (min)
<i>Euschistus ictericus</i> (11)	271.5 (46.0) <sup>B</sup>	741.4 (176.0) <sup>C</sup>
<i>Euschistus politus</i> (16)	90.6 (16.3) <sup>A</sup>	84.8 (17.0) <sup>A</sup>
<i>Euschistus servus</i> (11)	348.8 (43.1) <sup>B</sup>	538.1 (104.9) <sup>BC</sup>
<i>Euschistus tristigmus</i> (19)	252.2 (33.3) <sup>B</sup>	589.7 (56.1) <sup>BC</sup>
<i>Euschistus variolarius</i> (14)	119.2 (24.4) <sup>A</sup>	407.4 (48.2) <sup>B</sup>
<i>Thyanta custator accerra</i> (9)	117.8 (23.8) <sup>A</sup>	683.7 (77.9) <sup>C</sup>

<sup>a</sup>Values are presented as means  $\pm$  1 S.E.M. Means in each vertical column not marked with the same superscript letter are significantly different at the 0.02 level using Tukey's w-procedure.

2). There was an overlapping pattern of statistically significant differences; *E. politus* had a shorter duration than any of the other species. *E. ictericus* and *T. c. accerra* both remained in the copulatory linkage longer than *E. variolarius*. *E. servus* and *E. tristigmus* were intermediate in copulation duration.

For *E. politus*, the precopulatory mating sequence involved a rapid set of antennal palpations starting from the head of the female and progressing toward the rear of the abdomen. The single sequence usually involved male antennal and head contact only with the sides and rear of the female's abdomen; no contact was made with the head or thorax of the female. Near the end of the palpation and head contact phase, males often made distinct head butts to the sides and rear of the female's abdomen. In the process the male would back away and then rapidly move toward and slightly underneath the female, lifting her posterior off the substrate. Then the male would turn and achieve intromission without making contact with the female while turning; males were almost always successful on their first attempt. Mating sequences were short and the duration of the copulatory linkage was brief (Table 2).

*Euschistus tristigmus* varied considerably in palpation and head contact; the sequence was both head-to-rear and vice versa depending on the individual mating. There was more antennal palpation of the female's head by the male than in any other species examined. This first phase involved palpation and head contact with the female's head, thorax and abdomen. Just prior to turning around, the male generally used his head to push the rear of the female's abdomen upward. Most males then turned slowly, out of contact with the female, and attempted intromission. However, three males remained in contact with the female during the turning phase, sliding the rear of their abdomen along the side of the female until achieving the end-to-end position. Most, but not all, sequences involved two or more complete cycles involving antennation, head contact and turning prior to achieving successful intromission. Sequences were relatively long and the duration of the copulatory linkage approached those of longest duration among the species tested (Table 2).

In *E. ictericus*, all but one sequence involved a pattern of antennal palpation and head contact that was initiated at the head region of the female and progressed to the rear. The antennation was directed at the head, thorax and abdomen of the female, but head contact occurred only with the latter two body regions. Males turned to attempt intromission without making contact with females. A majority of males engaged in two or more complete sequences before achieving intromission. The mating sequence was relatively long, and duration of the copulatory linkage was one of the longest among the six species we examined (Table 2).

For *E. variolarius*, all of the antennal palpation and head contact portions of the precopulatory mating sequence began, with one exception, at the head region and progressed to the rear of the abdomen. There was a great deal of variation with regard to where male palpation and head contact occurred on the female's head, thorax and abdomen with no clear pattern. Two of the males exhibited head butting of the female similar to that seen in *E. politus* (i.e., only along the abdomen). Only one complete mating sequence occurred for each pair. The male turned to achieve intromission without maintaining contact with the female. Overall, mating sequences were short and the duration of the copulatory linkage was intermediate relative to the other species (Table 2).

Most male *E. servus*, performed only one mating sequence before intromission; most but not all made both antennal palpation and head contact with all three body regions of the female. We observed more palpation of the thorax than in the other species. In three pairs, the male lifted the rear of the female's abdomen as seen in *E. tristigmus*. The overall mating sequence for this species was quite long, including lengthy bouts of palpation. Duration of

the copulatory linkage was intermediate relative to the species examined (Table 2).

For *T. c. accerra*, there was a single mating sequence for a majority of the pairs. With one exception, males started their antennal palpation and head contact with the rear of the female's abdomen and progressed toward the head. The male's antennal and head contact with the head, thorax and abdomen of the female varied more in these pairs than in any of the *Euschistus* species examined. Some males made antennal and head contact with all three regions of the female's body, but others made antennal contact with all three regions and head contact with only one or two regions, etc. One male exhibited head butts similar to those recorded for several of the other species. All of the males except one turned to attempt intromission without remaining in contact with the female; the exceptional male slid the rear of his abdomen along the outer edge of the female's thorax and abdomen as he turned. The mating sequence was short, but the duration of the copulatory linkage was among the longest of the species we tested (Table 2).

### DISCUSSION

Three conclusions emerge from our study: (1) Mating behavior patterns of the six sympatric stink bug species are each unique in some aspect or combination of aspects. Thus, it is possible that the behavior patterns could be part of a set of cues used for species recognition. (2) Several features of the mating patterns suggest that different general mating strategies exist in stink bugs. (3) Behavior patterns could be used to distinguish species when the total set of behavior patterns is examined, but not when any one feature of the mating sequence is used.

Our observations corroborated many of the mating behavior patterns reported by previous investigators examining pentatomid reproductive behavior. We agree with Alcock (1971) that the mating sequences in this group are diverse; however, we did note some similarities. For example, in none of the species we examined did males arrive at the copulatory position by climbing over the female nor did males ever occupy any type of male-above position. In all cases, males turned 180° to arrive at the end-to-end copulatory position.

If only the three precopulatory aspects of the mating sequence for the six species examined are considered, it is possible to distinguish all six from one another. They differ in the number of sequences, the direction along the female's body of the male's antennal palpations and head contact, and the total time from initiation of the sequence to copulatory linkage (Table 3). Because these six species are sympatric (McPherson, 1982) and sometimes even occur on the same types of vegetation (e.g., *Verbascum thapsus*; McPher-

Table 3.— Summary of the primary mating sequences of six species of stink bugs.

Species	No. Sequences	Direction	Latency to Lock	Duration of Lock
<i>Euschistus politus</i>	1	head to rear	short	short
<i>Euschistus tristigmus</i>	2+	both	long	intermediate/long
<i>Euschistus ictericus</i>	2+	head to rear	long	long
<i>Euschistus variolarius</i>	1	head to rear	short	intermediate
<i>Euschistus servus</i>	1	head to rear	long	intermediate/long
<i>Thyanta custator accerra</i>	1	rear to head	short	long

son and Mohlenbrock 1976), it may be important for females to discriminate male conspecifics from heterospecific males to avoid unnecessary copulations and gamete wastage. Quantitative data plus additional qualitative differences noted in some species, e.g., head butts, or total amount of antennal palpation, suggest that such discriminations are possible for all six species. Apparently, no previous studies have dealt with as large a number of sympatric species; our data suggest that additional studies of this sort are needed.

The rapid mating sequences of *E. politus* contrast with those of the other *Euschistus* species we examined (Table 3). The short duration of the precopulatory mating sequence coupled with brief copulatory linkages suggests that, for this species, the mating strategy involves multiple copulations by both males and females. For *E. variolarius* and *T. c. accerra* the mating sequences were also of short duration, but the copulatory linkages were intermediate or long. In these latter two species, and certainly in the other three species of *Euschistus*, the long copulatory linkage might be a type of mate guarding.

The data we collected exhibit enough variation in behavior among the five *Euschistus* species, and between them and *T. c. accerra*, to warrant investigation of additional taxa with the ultimate goal of a cladistic analysis. Further understanding of the evolutionary relationships within the Pentatomidae, and between this family and other groups of bugs, could be gained by such an approach.

Lastly, we must note that mating sequences in stink bugs, which we studied primarily from the perspective of the males' actions, involve response by the females as well. In many stink bug species, a receptive female will lift her abdomen at the appropriate point in the mating sequence, which is necessary before the male turns around and attempts aedeagal insertion (e.g., Alcock 1971, Fish and Alcock 1973, Vangeison and McPherson 1975, Youter and McPherson 1975). We observed similar behavior in females of several of the species we tested. An unreceptive female will not lift her abdomen (e.g., Cuda and McPherson 1976, Youter and McPherson 1975) and may actually kick the male (Youter and McPherson 1975). When the sexes interact behaviorally, some reciprocal stimulation could lead to acceptance (or rejection) of the male by the female and a successful copulation (or no copulation). Though likely part of mate location or mate choice, the calling recorded for *N. viridula* (Harris et al. 1982) could also involve reciprocal stimulation between the sexes. These sorts of phenomena have been reported for a variety of insects (Thornhill and Alcock 1983), although the proximate details of physiological changes for each member of the mating pair have not been studied in detail.

#### ACKNOWLEDGMENTS

We thank Heather Rice and Stephen Taylor for assistance with maintaining the stink bugs and Heather Rice for helping analyze the videotapes. This research was supported in part by funds from the College of Science at Southern Illinois University at Carbondale. We are grateful to the U. S. Forest Service (Harrisburg, IL) for permission to obtain stink bugs from the La Rue-Pine Hills Ecological Area. We also thank two anonymous reviewers for valuable comments on an earlier version of the manuscript.



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