

Male Courtship Before and During Copulation in Two Species of *Xyonysius* Bugs (Hemiptera, Lygaeidae)

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ABSTRACT: Males of two species of *Xyonysius* court females both before and during copulation. Courtship during copulation ("copulatory courtship") is more elaborate, and differs between the two species. Male genital sclerites are moved in ways suggesting that they stimulate females during copulation. It is argued that copulatory courtship may be under sexual selection by cryptic female choice.

Mating behavior in lygaeids is little studied, and most of what has been written concerns male mate location (e.g., Sweet, 1964 in Thornhill and Alcock, 1983), and male behavior leading to copulation (Carayon, 1964 in Thornhill and Alcock, 1983). This paper describes courtship that occurs both prior to and during copulation in *Xyonysius californicus* (Stal), and *X. sp. nr. basalis* (Dallas). *X. californicus* is considered a pest of guayule (*Parthenium argentatum*—Asteraceae), a source of rubber of potential economic importance (Stone and Fries, 1986). We know of no previous descriptions of male mating behavior in this genus.

Male courtship behavior has traditionally been thought to function to induce females to allow males to copulate with them (Darwin, 1871). Recent studies, however, have shown that male courtship behavior is also commonly performed after copulation has already begun (Eberhard, 1991, in press). The proposed function of such "copulatory" courtship is to induce females to behave in ways that increase the male's chances that his gametes will be used to father her offspring (open internal valves to allow him deeper access, transport his sperm to storage sites, discard sperm from previous males, refrain from discarding his sperm, etc.) (Eberhard, in press). If this interpretation is correct, then copulatory courtship is probably often under sexual selection by female choice ("cryptic" female choice—Thornhill, 1983).

One prediction which follows from this interpretation is that, since characters under sexual selection by female choice often diverge rapidly in closely related species (West-Eberhard, 1983), copulatory courtship should often differ among congeneric species. This paper tests this prediction for two species of *Xyonysius*.

Materials and Methods

Individuals of *X. californicus* were captured in May, 1991 by sweepnetting in a pasture and at a light trap, on which they were found mating near Punta Morales (el. 10 m), Puntarnas Province, Costa Rica. Mating behavior was observed in San José at room temperature in petri dishes under a dissecting microscope (7×). The behavior of some pairs was videotaped using a National Omnipro camera

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with +6 closeup lenses (30 images/sec). Individuals of *X. sp. nr. basalis* were collected on flowers of *Montanoa* sp. (Compositae) near San Antonio de Escazu (el. 1300–1400 m), San José Province, Costa Rica and taped and observed at room temperature in petri dishes under a microscope (8×, 20×, 40×).

The angles of observation and portions of copulations which were observed varied in both species. Sample sizes given below refer to the number of times couples were in a position that allowed particular movements to be seen, and do not necessarily reflect their frequency of occurrence. Voucher specimens are deposited in the Instituto Nacional de Biodiversidad in Santo Domingo de Heredia, Costa Rica, and in the Museo de Insectos of the Universidad de Costa Rica. Drawings of behavior were traced from video images. Structures not clear in the video (e.g., antennae out of the plane of focus) were omitted.

Results

XYONYSIUS CALIFORNICUS: When two individuals met, they usually walked over each other or passed by without responding. They sometimes paused momentarily with legs I and II of one side over the other's back. Twice individuals raised their legs III in response to nearby individuals.

Several copulation attempts, one nearly complete mating, and 15 copulations with the initial portion missing (4 taped) were observed. A total of 31 min from four copulations was taped. Male sexual behavior began when the male mounted the female facing in the same direction, with all his legs on her body. The female usually (in all but one case) tried to dislodge the male by swinging her body from side to side, or by rubbing her legs III against the sides of her wings and the male's legs III (four cases) (Fig. 1). While in this position, the male vibrated his antennae over the female's head and pronotum, apparently touching her repeatedly. In many cases the male then dismounted and left.

Only one male was observed as he shifted from this preliminary position to initiate genitalic contact. He stood alongside and a little behind the female, with his legs I and II still on her wings (Fig. 1), and he inserted his aedeagus between the sheaths of her ovipositor. In one case the male's parameres were pressed against the ovipositor during penetration. The male then turned 180° to face away from the female (Fig. 2). Often he kept his legs III raised while his other legs were on the ground. When the female walked, the male followed her.

Males performed three different behavior patterns during copulation that appeared to be designed to stimulate the female. The male repeatedly rubbed the female's wings and posterior abdominal sternites with his tarsi III (Fig. 2) in at least 11 of 14 pairs, in bursts of activity that lasted from 1–6 sec ($\bar{x} \pm SE = 2.34 \pm 0.21$, $n = 32$); times between bouts of rubbing varied from 1 to 249 sec. The male also vibrated his parameres intermittently against the female's ovipositor, or repeatedly pressed them against it ($n = 3$ pairs for both behavior patterns). In addition, one male turned twice to a position alongside the female and briefly rubbed her dorsum with his legs II and her abdominal tergites with his legs III while maintaining genitalic coupling. The second time the male did this, the female tried to kick him, and he quickly turned away and rubbed her abdomen with his legs III.

A flow of material that lasted for several seconds, moving toward the female within the ovipositor, was seen in two pairs. In one case it occurred just after the

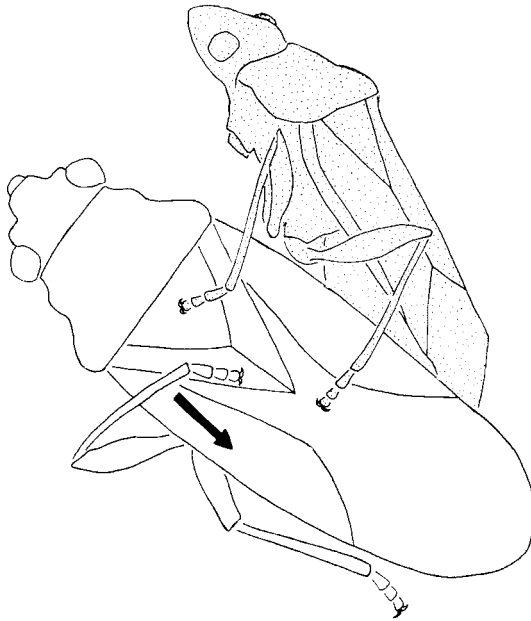


Fig. 1. Initial stage of copulation in *Xyonysius californicus*, with male (stippled) mounted on female. The female attempts to rub the male off with one leg III (arrow).

male had turned away from the female and was pressing her ovipositor with his parameres. In the other case there were small pulsations in the area near the base of the ovipositor.

In one pair, the female pulled on her ovipositor and the male's aedeagus by walking away from him. She then performed five quick pulls and recoils in 3 sec before returning to her former position. This happened 5:22 min after copulation began, in a 19:28 min copulation. In this same pair the male pulled in the forward direction (away from the female) for 4 sec (from 7:51 to 7:55), and then went back to following her and being dragged.

When another bug approached a mating couple, the male kicked with his legs III ($n = 5$) (Fig. 3). Mating females also kicked upwards ($n = 3$). Mating ended when the male walked away from the female, pulling out his aedeagus, which was $>30\%$ the length of the male's body. Once a male was observed slowly sheathing his aedeagus and rubbing it with his parameres. Durations of 15 copulations averaged $10:25 \pm 3:21$ ($N = 7$), and ranged between 2:05 and 25:35 min.

XYONYSIUS SP. NR. *BASALIS*: Portions of 13 copulations (three complete) involving 13 different pairs of bugs were observed; four of these (one complete) were taped for a total of 60 min.

In many respects behavior was similar to that of *X. californicus*. The male mounted the female facing in the same direction, tapped her rapidly and softly with his antennae, and the female waggled her body in apparent attempts, sometimes successful, to dislodge him. After achieving genitalic coupling (below), the male dismounted and turned to face away from the female.

In one pair a favorable angle of observation allowed detailed observations of intromission. The female's ovipositor was lodged in the male's pygophore, and

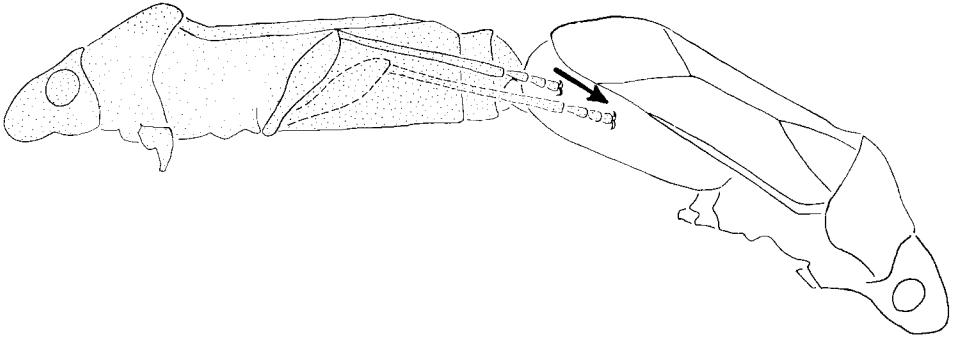


Fig. 2. A male *X. californicus* (stippled) rubs and taps the female with his legs III during copulation. The time between successive positions of the male leg III was 0.2 sec.

small dark genitalic structures of the male (presumably the parameres) manipulated the tip of the ovipositor continuously for 30–60 sec. Then a clear structure (or material) passed smoothly up the ovipositor and into the female's body, and this was followed by a more or less ball-like mass of complex brown sclerites, which took an estimated 10–15 sec to move smoothly from the tip of the ovipositor to its base. As the mass reached the base of the ovipositor, the male dismounted and began to turn to face away from the female. Within 30 sec the brown mass had moved slightly deeper into the female, and was only partly visible.

Apparent male courtship during copulation that was similar to behavior of *X. californicus* included bursts of tapping or rubbing on the ventral and lateral surfaces of the female's abdomen (and occasionally the undersides of her wings) with both legs III (seen in all pairs). The legs did not tap simultaneously; they sometimes moved in clear alternation (Fig. 4), but more often did not.

The male also occasionally turned briskly to grasp the female and stroke her with one leg III on her dorsal surface while the other leg III rubbed the ventral surface of her abdomen (Fig. 5) (seen in five pairs, certain not to have occurred in one other). The upper leg III sometimes extended over the edge of the female's body, and rubbed her ventral surface with the tip of the tibia. The lower leg rubbed in an anterior-posterior motion; the upper leg also rubbed in this direction as well

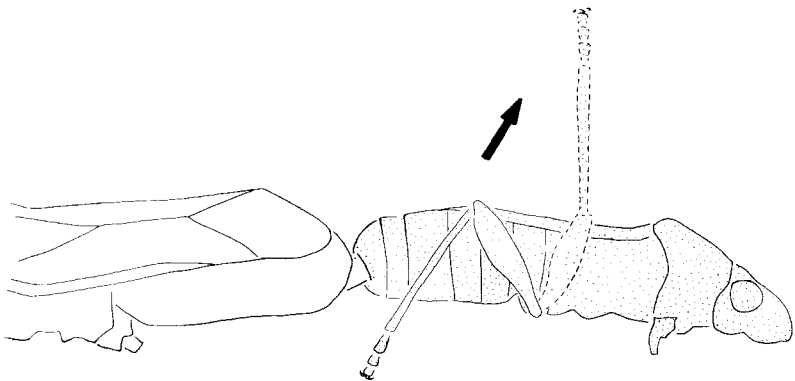


Fig. 3. A copulating male *X. californicus* (stippled) kicks at a nearby bug with his leg III. Time between successive positions of the leg was 0.6 sec.



Fig. 4. A copulating male *X. sp. nr. basalis* (stippled) taps and rubs the female with his legs III (arrows). After several more taps, he pushed the female with his legs III (Fig. 7). Time between successive positions of legs III was 0.1 sec.

as laterally. The duration of six taped bursts of rubbing averaged 3.8 ± 0.6 sec. Legs I and II also shifted positions frequently on the female's dorsal surface, but appeared not to rub her. In all cases this type of rubbing ended when the female waggled her abdomen energetically.

The male's parameres also pressed rhythmically on the dorsal surface of the ovipositor (seen in six pairs) (Fig. 6). The male's genital capsule moved slightly posteriorly with each pressing movement of the parameres. Close observation of paramere movements revealed further details. In four pairs the parameres occasionally vibrated rapidly in an approximately horizontal plane. The vibrations occurred during pauses in bursts of rhythmic pressing movements (e.g., Fig. 6). During most (but not all) bursts of vibration, the distal portions of the parameres apparently rubbed against the dorsal surface of the female's ovipositor. The long setae on the basal surfaces of the parameres also contacted the female's abdomen (Fig. 6), and moved against it as the parameres moved.

An additional behavior pattern, not seen in *X. californicus*, consisted of the male pushing the female's abdomen repeatedly with both his legs III simultaneously so her ovipositor was pulled away from her body and the tips of the two bugs' abdomens were briefly out of contact (Fig. 7). The male's legs III often quivered as they pushed the female. Pushing behavior, seen in 12 of 13 pairs, was usually associated with tapping.

On five occasions a pair which had been isolated for observation was seen copulating a second time within two hours.

Discussion

Using the criteria of repeatability, stereotypy, rhythmic repetition, appropriate design to stimulate the female, and mechanical irrelevance for maintaining the male's grip on the female (Eberhard, 1991, in press), several behavior patterns performed by male *Xyonysius californicus* and *X. sp. nr. basalis* prior to and during copulation appear to be courtship. Some of the behavioral patterns differed between the species, and others were similar:

ANTENNAL TAPPING: Males of both species tapped the female in a similar fashion.

INTROMISSION: The moment of genitalic coupling was observed in more detailed in *X. sp. nr. basalis* than in *X. californicus*; differences in the descriptions do not necessarily reflect differences between the species.

RUBBING WITH HIND LEGS WHILE TAIL-TO-TAIL. Males of both species performed

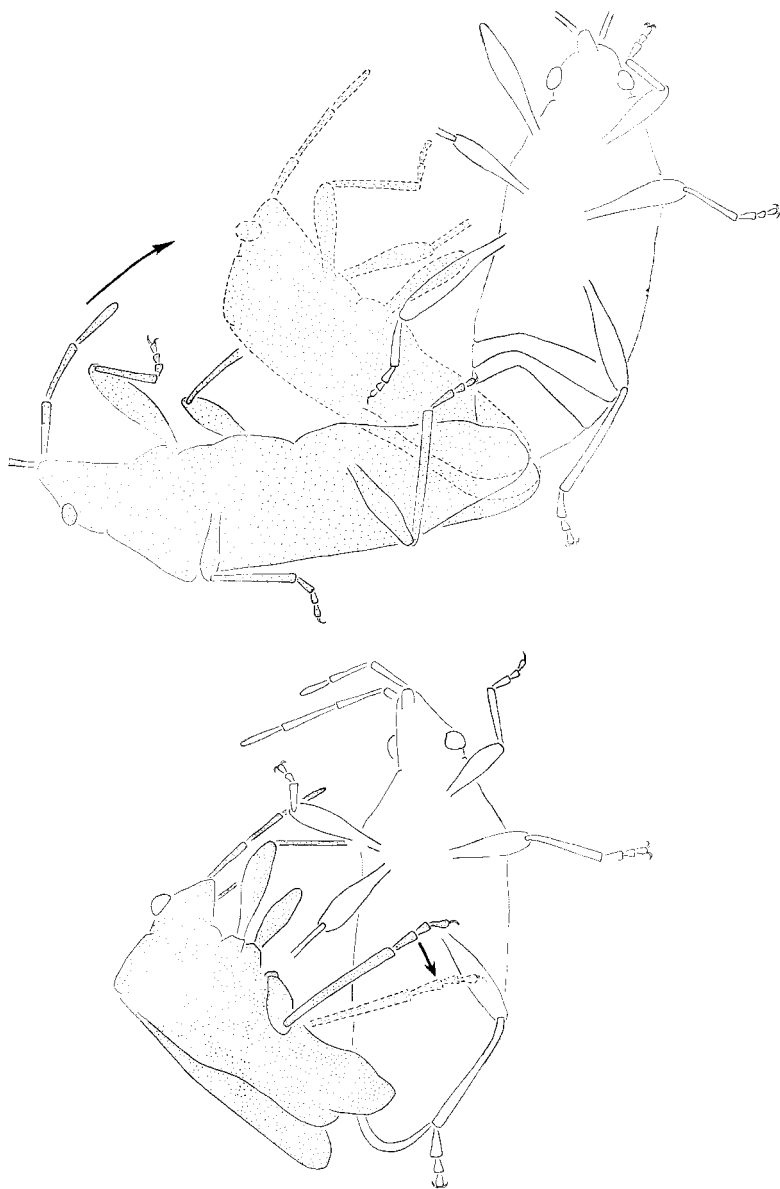


Fig. 5. A copulating male *X. sp. nr. basalis* (stippled) turns briskly to seize the female (above) (time between successive positions was 0.43 sec). The male then rubs the female's abdomen vigorously with his legs III (below) (time between successive positions was 0.07 sec). The other leg III (out of sight in this ventral view) rubbed on the female's dorsal surface at the same time.

bouts of similar rubbing and tapping motions. Males of *X. californicus* were not observed with enough detail to determine whether their legs moved in alternation or simultaneously.

RUBBING FEMALE WHILE FACING IN SAME DIRECTION. Males of *X. californicus* rubbed the female's dorsum with legs II and her abdomen with legs III, while

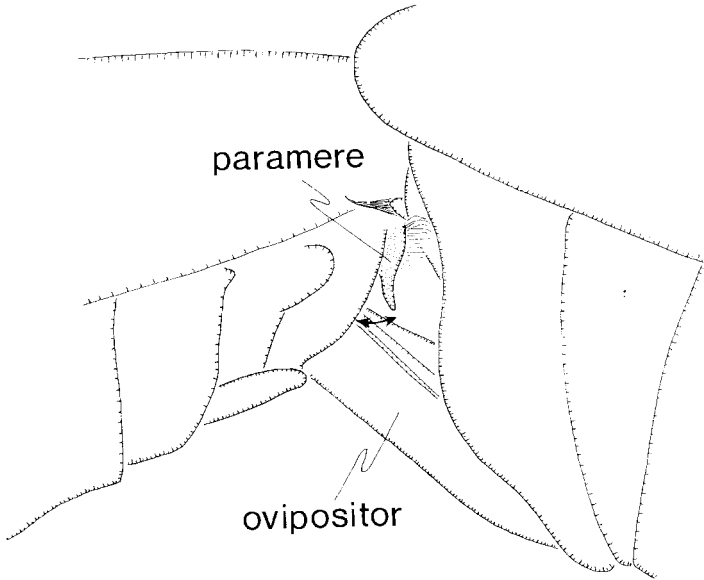


Fig. 6. Schematic view of pressing movement of parameres (stippled) of a male *X. sp. nr. basalis* on the dorsal surface of the female's ovipositor during copulation. Seta on the parameres brushed against the posterior surface of the female's abdomen. Pressing movements occurred about once every 0.5 sec. Drawn from a pair frozen during copulation and video recordings.

those of *X. sp. nr. basalis* differed in stroking the female's dorsal surface with one leg III while the other rubbed the ventral side of her abdomen.

TAP OVIPOSITOR WITH PARAMERES. Tapping or pressing with the parameres occurred in both species; *X. sp. nr. basalis* was observed in more detail, and differences between the species are not certain.

PUSH FEMALE WITH HIND LEGS. This behavior was common in *X. sp. nr. basalis*, but was never seen in *X. californicus*.

The differences in copulatory courtship between these species is in accord with the prediction that rapid divergence will be common for behavior that is under sexual selection by female choice. Courtship behavior may have several functions. Pre-copulatory antennal tapping may induce the female to accept intromission. Rubbing and tapping the female with legs III, and turning to grasp and rub her may help keep her still, or inhibit her from attempting to reject the male. The observation of a male *X. californicus* that began to tap in response to kicks by the female suggests such a function.

Male parameres were moved rhythmically in two and probably three different ways during copulation. They almost certainly stimulate the female both when their tips squeeze the ovipositor, and probably also as they vibrate against the dorsal surface of the ovipositor. They also apparently knead the tip of the ovipositor after it has been clamped in the pygophore just prior to intromission, at least in *X. sp. nr. basalis*. In addition, the long setae at the bases of the parameres rub against the tip of the female's abdomen.

Female *X. sp. nr. basalis* copulated repeatedly. The frequency of copulation in *X. californicus* suggests that the females of this species also remate. Multiple mating

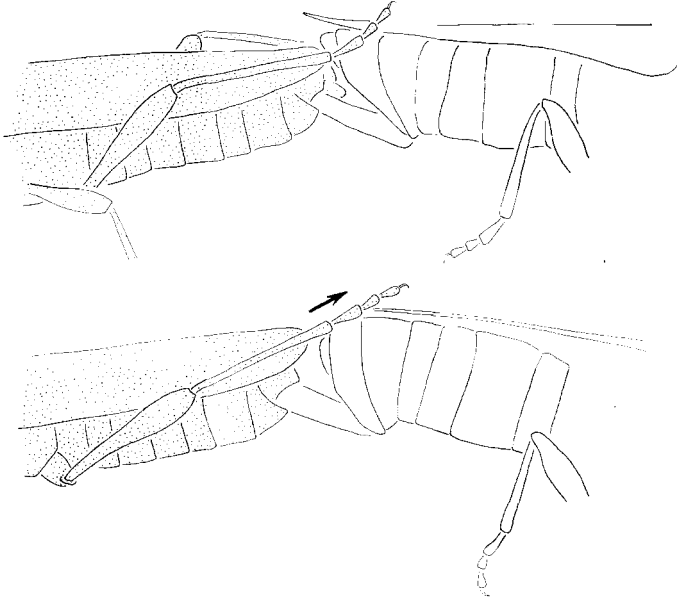


Fig. 7. A copulating male of *X. sp. nr. basalis* (stippled) pushes on the female's abdomen with his legs III (arrow), causing the tips of their abdomens to separate and pulling the female's ovipositor away from her body. Bottom drawing followed top by 0.6 sec.

by females has also been documented for other lygaeids (Sillén-Tullberg, 1981 *in* Thornhill and Alcock, 1983). Cryptic female choice, which is expected only when females mate repeatedly (Eberhard, 1990), is thus a possible explanation for the copulatory courtship behavior of these species.

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Literature Cited

- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex* (reprinted). Random House, New York.
- Eberhard, W. G. 1990. Animal genitalia and female choice. *Am. Sci.* 78:134-141.
- Eberhard, W. G. 1991. Copulatory courtship and cryptic female choice in insects. *Biol. Rev.* 66: 1-31.
- Eberhard, W. G. In press. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution*.
- Eberhard, W. G., and S. Kariko. Submitted. The inside and the outside of copulation in the beetle *Macrohaltica jamaicensis* (Coleoptera: Chrysomelidae). *J. Ins. Behav.*

- Stone, J. D., and J. N. Fries. 1986. Insect fauna of cultivated guayule, *Parthenium argentatum* Gray (Campanulatae: Compositae). *J. Kans. Ent. Soc.* 59:49-58.
- Thornhill, R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus apicalis*. *Am. Nat.* 122:765-788.
- Thornhill, R., and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard Univ. Press, Cambridge.
- West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Quart. Rev. Biol.* 58:155-183.