

Male and Female Mating Behavior in Two *Ozophora* Bugs (Heteroptera: Lygaeidae)

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ABSTRACT: Mating behavior in *Ozophora* lygaeid bugs is described for the first time. Male and female copulatory behavior differed between *O. baranowskii* and *O. maculata*. Females tapped or pushed the males with their hind legs during copulation. In *O. baranowskii* female tapping was inversely correlated with copulation length, and male copulatory courtship occurred in association with tapping. Females sometimes ejected a spermatophore containing live sperm after copulation.

Male behavior that stimulates the female during mating, copulatory courtship, occurs frequently among insects and spiders (Eberhard, 1991, 1994), probably to influence cryptic female choice, which occurs during or after copulation (Thornhill, 1983; Eberhard, 1991, 1994, 1996). Male post-copulatory courtship influenced sperm storage and use by the female in the fly *Dryomyza anilis* (Otronen and Siva-Jothy, 1991; Otronen, 1997). On the other hand, female behavior that apparently stimulates the male during mating is much less frequent. For example, it occurred in only 5% of 132 species included in a study with detailed observations of mating on insects and spiders (Eberhard, 1994). But the surprising thing is that such behavior occurs at all, because it is usually the male that must try to induce favorable responses in the female.

This paper gives a detailed description of the mating behavior of two lygaeid bugs, *Ozophora baranowskii* Slater & O'Donnell and *Ozophora maculata* Slater & O'Donnell. In both species the female touched the male during copulation in an apparently stimulatory manner. This is the first description of mating behavior for *Ozophora* bugs, which are often seed predators of figs (Slater, 1972). Details of behavior are used to evaluate explanations for male and female copulatory behavior.

Materials and Methods

Bugs were collected near San Antonio de Escazú (el. 1300–1400 m), San José Province, Costa Rica, in an area of coffee plantations and secondary forest. Adults were captured from branches of *Ficus padifolia* (Moraceae) trees and from the ground below them, where nymphs were also found. Rearing methods are described in Rodríguez S. (1997). Last instar nymphs and adults were kept each in a Petri dish.

Lab-reared females were not mated until after eight days post-molting to avoid the risk of increased early mortality sometimes associated with early copulation, as in the lygaeid *Oncopeltus fasciatus* (Loher and Gordon, 1968). Matings were observed in Petri dishes under a dissecting microscope. Keeping the Petri dish on a mirror, it was possible to observe some internal genitalic behavior during copulation through the partially transparent female ovipositor. Verbal descriptions were dictated to a tape

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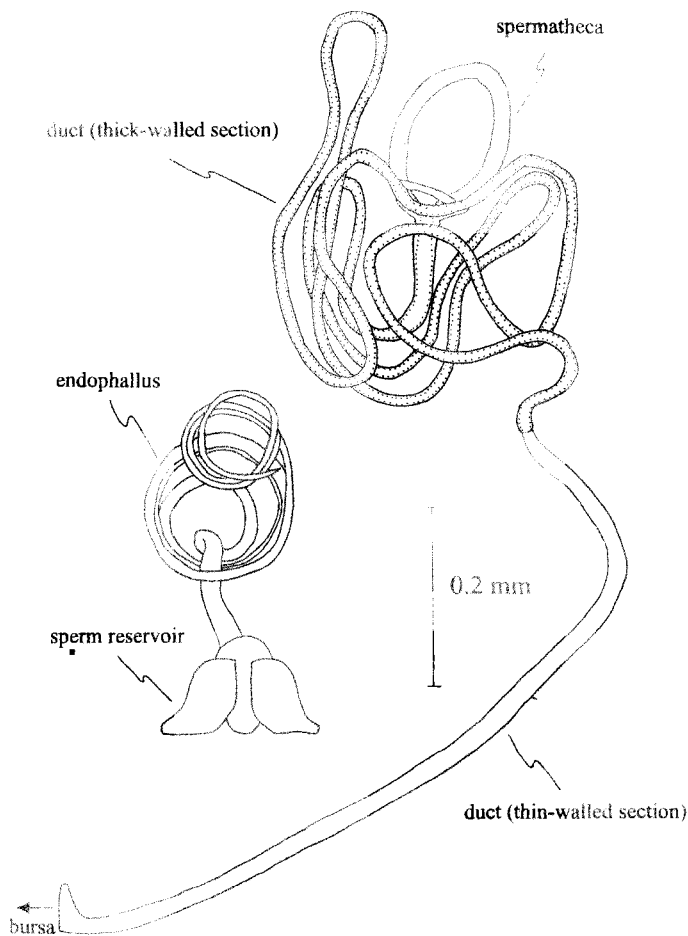


Fig. 1. Male endophallus and sperm reservoir, and female spermatheca and spermathecal duct in *O. baranowskii*. Terminology is after Slater (1983a, b). The dotted line inside the spermathecal duct shows the thick-walled section, which had a band of muscle around it (not shown).

recorder. After each mating the male was removed from the Petri dish and the female observed for 30 min to check for spermatophore ejection.

Six *O. baranowskii* pairs and one *O. maculata* pair were frozen in copula with liquid nitrogen. Other *O. baranowskii* couples were immobilized with ethyl chloride spray ($n = 6$) or molten paraffin ($n = 3$). Pairs frozen with nitrogen or ethyl chloride were kept in 70% Ethanol at -5°C for a month before dissection for the tissues to harden.

Averages are given \pm the standard error (SE). Except if otherwise indicated two-tailed Mann-Whitney U -tests were used to analyze data. When several statistical tests were made with the same data set, the sequential Bonferroni technique (Rice, 1989) was used to avoid spurious significance. Voucher specimens were deposited at IN-Bio (Instituto Nacional de Biodiversidad), Santo Domingo de Heredia, Costa Rica.

Results

When placed in a Petri dish the bugs walked rapidly and tried to escape, calmed down after a few minutes and began to walk slowly or remained still until another

Table 1. Female tapping and pushing in *O. baranowskii* and *O. maculata*. To compare episode length, averages per copulation were used as data points. Both *P* values are significant after the Bonferroni correction.

	Episodes per copulation		Episode length (sec)		Incidence (sec/min)	
	av \pm SE	range	av \pm SE	range	av \pm SE	range
<i>O. baranowskii</i> <i>n</i> = 50	18 \pm 2	4–69	46 \pm 5	5–203	16 \pm 2	1–60
<i>O. maculata</i> <i>n</i> = 10	17 \pm 5	1–48	20 \pm 6	5–60	4 \pm 2	1–15
			<i>P</i> = 0.005		<i>P</i> = 0.004	

bug walked by. When two females met they walked away from each other. Sometimes a male mounted another male and touched the other's genital capsule with his own, but dismounted after a few seconds. In *O. baranowskii* there were 100 male-female copulation attempts that resulted in 53 copulations (18 of wild-caught individuals, 27 of virgin females, 8 second copulations of these females). With wild-caught *O. maculata* there were 18 attempts resulting in 13 copulations. Sample sizes below vary because not all movements could be observed equally well in all copulations.

A male attempted copulation by mounting a female facing in her direction, all his legs but one on her thorax and wings. The hind leg of the side from which he approached remained on the Petri dish. The male tapped the head, thorax and wings of the female with his antennae and legs, and backed down to couple his genitalia with her ovipositor, twisting his genital capsule by 180°. He introduced his endophallus and sperm reservoir (Fig. 1) through the valves of her ovipositor into her abdomen, dismounted and turned to face in the opposite direction. In *O. baranowskii* the male genitalia had entered the female abdomen by 53 \pm 4 sec of copulation (*n* = 45), and by 28 \pm 3 sec (*n* = 12) in *O. maculata*. The female often ran away or shook her body sideways when the male mounted.

O. baranowskii copulations lasted 65 \pm 9 min (range = 1–333 min, *n* = 52). *O. maculata* copulations were twice as long (118 \pm 13 min, range = 19–195, *n* = 13, *P* = 0.0006). Copulations usually ended when the male walked away pulling his genitalia out of the female. Only once in *O. maculata* did the female appear to cause separation by walking away. One *O. baranowskii* female died during copulation (she was alive at 3.3 hr of copulation, dead by 3.6 hr). But the male remained coupled until at least 5.5 hr, and had separated by the next check at 14 hr. This indicates the male can end copulation without participation from the female.

FEMALE BEHAVIOR: In both species the female touched the male during copulation with her hind legs (in all of 50 *O. baranowskii* copulations, in 10 of 11 *O. maculata* copulations). The movement differed between the two species. In *O. baranowskii* the female tapped the male and in *O. maculata* she pushed him (Fig. 2).

Tapping and pushing did not occur continuously, but in episodes throughout copulation. Tapping episodes in *O. baranowskii* were more than twice as long as pushing episodes in *O. maculata* (Table 1). The incidences per copulation of tapping and pushing were measured as seconds of tapping or pushing per min of copulation, for copulations in which they occurred. The overall incidence in *O. baranowskii* was significantly higher than in *O. maculata* (Table 1). The temporal pattern also differed

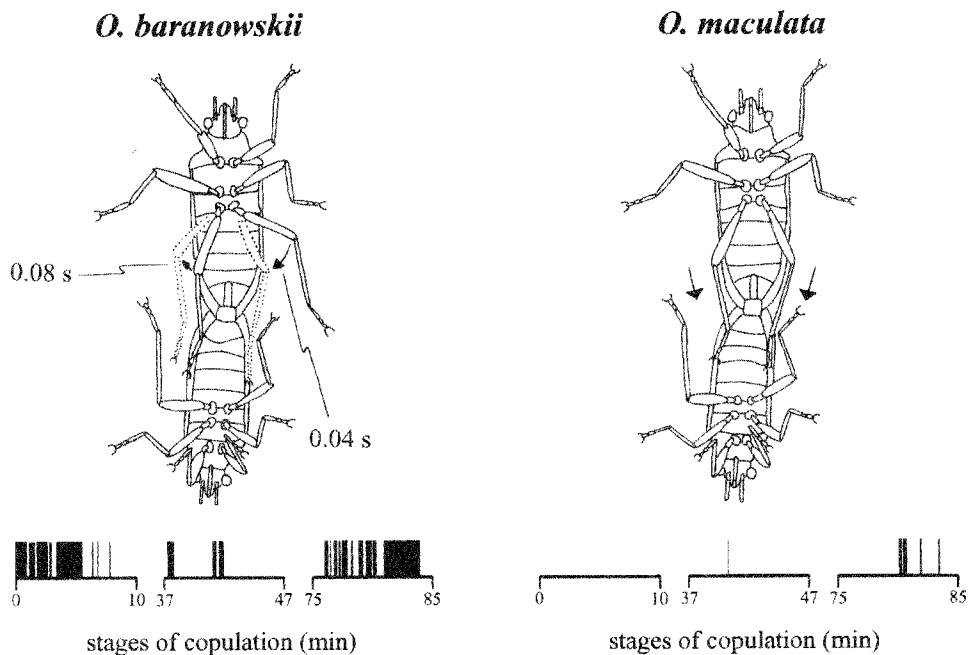


Fig. 2. Schematic drawing of the female movement of touching the male during copulation. In *O. baranowskii* the female softly tapped the male's abdomen, genital capsule, and wings with alternating movements of her hind legs (positions of hind legs traced from video images). In *O. maculata* she pushed his abdomen, genital capsule and wings with forceful, simultaneous movements of her hind legs. Black bars represent episodes of tapping or pushing during the first, middle and last 10 min periods of one *O. baranowskii* and one *O. maculata* copulation.

(Fig. 2). In *O. baranowskii* tapping often began just after the male dismounted after genital coupling (44 of 51 copulations), but this never happened in *O. maculata*. In *O. baranowskii* tapping incidence was highest at the beginning and end of copulation, while in *O. maculata* pushing occurred mostly at the end (Fig. 2, Table 2). At the beginning and end of copulation, the incidence of tapping was much higher in *O. baranowskii* than the incidence of pushing in *O. maculata* (Table 2).

Tapping or pushing were sometimes violent. In *O. baranowskii* strong taps resembled kicks and in *O. maculata* strong pushes stretched the genital capsule away from the male's abdomen. But neither the length of copulation nor the incidences of tapping or pushing differed significantly between copulations in which strong tapping or pushing occurred or not ($P > 0.24$ in both species). Sometimes the male placed his hind legs in the way of the female's legs (22 of 46 *O. baranowskii* copulations, 4 of 10 *O. maculata* copulations) but this did not appear to hinder her.

The female often shook her body sideways during tapping or pushing, more frequently in *O. baranowskii* (43 of 48 copulations) than in *O. maculata* (2 of 10 copulations, $G^2 = 19.65$, d.f. = 1, $P << 0.005$). Copulation length did not vary significantly between cases in which the female shook her abdomen or not ($P > 0.15$ for both species).

MALE BEHAVIOR: In both species the male performed up to three types of movement during copulation:

Table 2. Incidence (sec/min) of female tapping or pushing at different stages of copulation in *O. baranowskii* and *O. maculata*. Stages were measured in periods of 1/10th the average copulation length (65 min in *O. baranowskii*, 118 min in *O. maculata*). Thus, *O. baranowskii* tapping incidence was determined for the first, middle and last 6.5 min periods of each copulation (six copulations too short to be so divided were excluded from this analysis). *O. maculata* pushing incidence was measured in periods of 11.8 min. *P* values significant after the Bonferroni correction are indicated with an asterisk (*).

	Stages of copulation			Kruskal-Wallis test between periods	
	Beginning	Middle	End		
<i>O. baranowskii</i> <i>n</i> = 44	18 ± 2	3 ± 1	36 ± 3	<i>P</i> < 0.00001*	All periods different with Tukey's test
<i>O. maculata</i> <i>n</i> = 10	0.2 ± 0.1	0.4 ± 0.2	13 ± 6	<i>P</i> = 0.001*	Beginning and middle not different with Tukey's test
Mann-Whitney <i>U</i> -test					
between species	<i>P</i> < 0.0001*	<i>P</i> = 0.57 NS	<i>P</i> = 0.002*		

1) Mount the female (Table 3). Maintaining intromission the male re-mounted the female and tapped her head, thorax, wings and abdomen with his antennae and legs, then dismounted and returned to his position. Mounts were not more frequent in one species than the other (40 of 51 *O. baranowskii* copulations, 10 of 10 *O. maculata* copulations, $G^2 = 1.74$, calculated adding 1 to all categories, d.f. = 1, $P > 0.10$).

2) Tap wings of female. The male raised his hind legs simultaneously until perpendicular to the substrate, lowered them with circular movements and tapped the wings of the female 1–2 times. Sometimes the male did not touch the female (20 of 92 *O. baranowskii* leg raises, 11 of 18 *O. maculata* leg raises). The frequency of wing taps did not differ between species (25 of 51 *O. baranowskii* copulations, 4 of 11 *O. maculata* copulations, $\chi^2 = 0.11$, d.f. = 1, $P > 0.10$) but there was a higher incidence per copulation in *O. baranowskii* (Table 3).

3) Vibrate hind legs. In *O. maculata* leg vibration was strong and there were vibratory movements in the body of the male and the female in all of 10 copulations (sometimes visible without the dissecting scope). In *O. baranowskii* it was softer and vibratory movements were seen in the male or female in only 14 of 26 copulations ($G^2 = 6.24$, d.f. = 1, $P < 0.05$). Leg vibration was more frequent in *O. maculata* (all of 10 copulations) than in *O. baranowskii* (31 of 49 copulations, $G^2 = 4.51$, calculated adding 1 to all categories, d.f. = 1, $P < 0.05$). Episodes were longer but had a lower incidence per copulation in *O. baranowskii* (Table 3).

Incidences of male movements were not significantly correlated with each other (in all cases $r_s < 0.30$, $P > 0.05$) except *O. baranowskii* mounts and wing taps ($r_s = 0.56$, $n = 50$, $P < 0.001$, significant after the Bonferroni correction).

GENITAL MOVEMENTS: When the male genitalia moved through the female ovipositor the endophallus was coiled as in Fig. 1.

In *O. baranowskii* there were three pseudo-copulations that lasted 1–2 min in which the male genitalia remained at the distal tip of the ovipositor making small, rapid, back-and-forth movements (about 1–2/sec). Another case lasted 1.6 min and the male genitalia penetrated the female for only 15 sec. These copulations had sig-

Table 3. Male copulatory movements in *O. baranowskii* and *O. maculata*. To compare the length of mounts and of episodes of wing tapping and leg vibration between species, averages per copulation were used as data points. *P* values significant after the Bonferroni correction are indicated with an asterisk (*).

Mount female			
	Mounts per copulation	Mount lengths (sec)	Incidence (mounts/hr)
<i>O. baranowskii</i> <i>n</i> = 40	5 ± 1	6 ± 1	4.8 ± 0.6
<i>O. maculata</i> <i>n</i> = 10	5 ± 1	10 ± 2	2.4 ± 0.6
		<i>P</i> = 0.08 NS	<i>P</i> = 0.06 NS
Tap wings of female			
	Episodes per copulation	Episode length (sec)	Incidence (episodes/hr)
<i>O. baranowskii</i> <i>n</i> = 25	3 ± 0.4	2 ± 2	3 ± 0.6
<i>O. maculata</i> <i>n</i> = 4	1–2	4 ± 1	0.6 ± 0.06
		<i>P</i> = 0.04 NS	<i>P</i> = 0.006*
Vibrate hind legs			
	Episodes per copulation	Episode length (min)	Incidence (episodes/hr)
<i>O. baranowskii</i> <i>n</i> = 29	1 ± 0.1	27.3 ± 5.9	1 ± 0.2
<i>O. maculata</i> <i>n</i> = 10	29 ± 4	1 ± 0.2	13 ± 2
		<i>P</i> = 0.0009*	<i>P</i> < 0.0001*

nificantly higher tapping incidences (47 sec/min in one case, 60 sec/min in the others) than copulations in which the male genitalia entered the female abdomen for prolonged periods (Table 1, *P* = 0.002).

During copulation the male genitalia were sometimes withdrawn from the female's abdomen, made small, quick, back-and-forth movements between the tip of the ovipositor and the male genital capsule, and then re-entered. This was less frequent in *O. baranowskii* (13 of 49 copulations) than in *O. maculata* (10 of 11 copulations, $\chi^2 = 14.01$, d.f. = 1, *P* << 0.005). Withdrawals were significantly longer in *O. maculata* (Table 4).

In all pairs immobilized *in copula* (15 *O. baranowskii*, 1 *O. maculata*) the male endophallus was inside the female spermathecal duct. But it was inside the thick-walled section of the duct (Fig. 1) in only 1 of 11 pairs (in the other 5 the endophallus may have been pulled out during dissection). In all cases the male sperm reservoir was in the ovipositor, which was never seen in living pairs if the endophallus was inside the female's abdomen. Thus the males apparently had begun to retract their genitalia before immobilization and the penetration of the endophallus into the spermathecal duct may be under-estimated. Sperm transfer in *O. baranowskii* occurred after 30–45 min of copulation (Rodríguez S., 1998b).

Table 4. Withdrawals of the male genitalia from the female abdomen in *O. baranowskii* and *O. maculata*. To compare withdrawal length, averages per copulation were used as data points. The *P* value marked with an asterisk (*) is significant after the Bonferroni correction.

	Withdrawals per copulation	Withdrawal length(s)	Incidence (withdrawals sec/hr)
<i>O. baranowskii</i> <i>n</i> = 12	3 ± 1	30 ± 3	7.8 ± 3
<i>O. maculata</i> <i>n</i> = 10	10 ± 1	68 ± 12	4.8 ± 1.2
		<i>P</i> = 0.02*	<i>P</i> = 0.62 NS

In six *O. baranowskii* copulations the genitalia were observed when the pair separated. Twice the male genitalia remained inside the female abdomen until the last moment and in four cases they were withdrawn 1–35 sec earlier. In one *O. maculata* copulation they were withdrawn 9 sec earlier.

SPERMATOPHORE EJECTION: The female sometimes ejected a spermatophore (Fig. 3). This occurred 3–18 min (*n* = 3) after copulation in *O. baranowskii*, and 10.1 ± 1.5 min after copulation (range = 4–20 min, *n* = 10) in *O. maculata*. It was more frequent in *O. maculata* (10 of 13 copulations) than in *O. baranowskii* (14 of 51 copulations, $G^2 = 10.69$, d.f. = 1, *P* < 0.05).

Seven *O. baranowskii* ejected spermatophores were examined under the microscope and five were full of living sperm (the other two had no sperm and one was full of what seemed oil droplets). All of six *O. maculata* ejected spermatophores were full of living sperm. The length of an *O. maculata* sperm measured with an optical grid on a microscope was 0.88 mm.

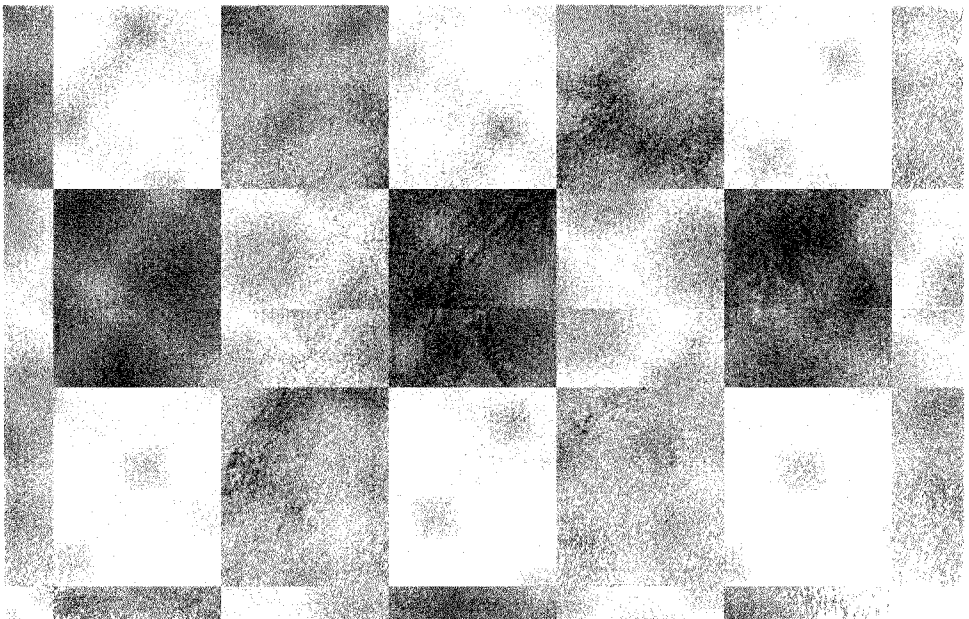


Fig. 3. Micrograph of a spermatophore ejected by an *O. maculata* female after copulation. When crushed by the coverslip, living sperm emerged from the central, round, transparent section of the spermatophore.

Table 5. Male behavior during copulation in relation to female tapping in *O. baranowskii*. The average incidence of tapping was 16 sec per 60 sec of copulation = 0.27. This was the null expectation for the proportion of male movements initiating during tapping episodes.

	Mounts		Wing tapping	
	Observed	Expected	Observed	Expected
During tapping episodes	66	50.49	23	20.52
When female was not tapping	121	136.51	53	55.48
	$\chi^2 = 6.53$, d.f. = 1, $P < 0.01$		$\chi^2 = 0.41$, d.f. = 1, $P > 0.10$	

O. baranowskii copulations after which the female ejected a spermatophore were significantly longer than copulations after which she did not (Fig. 4). The incidences of tapping, male movements and genitalia withdrawals did not differ significantly according to whether the female ejected a spermatophore in either species (in all cases $P > 0.05$).

ASSOCIATION BETWEEN MALE AND FEMALE BEHAVIOR: Male mounts and wing taps were classified as initiating within or without episodes of female tapping or pushing. Leg vibration episodes were too long to be so classified. For mounts and wing taps, there were no cases in which movements occurred partly within an episode of tapping or pushing, so movements that initiated or not during episodes actually occurred wholly within or without them.

O. baranowskii mounts occurred more frequently than expected during tapping episodes (Table 5) and during the second half of the episodes (22 mounts in the first half, 39 in the second, $\chi^2 = 4.74$, d.f. = 1, $P < 0.05$). Mounts occurred in longer tapping episodes (Fig. 5) and more mounts occurred in longer episodes ($r_s = 0.49$, $n = 51$, $P < 0.001$). All *O. maculata* mounts and wing taps occurred when the female was not pushing.

Male mounts were sometimes hindered by tapping or pushing, more frequently in *O. baranowskii* (44 failures in 225 attempts during tapping) than in *O. maculata* (3 failures in 62 attempts, $\chi^2 = 7.68$, d.f. = 1, $P < 0.01$).

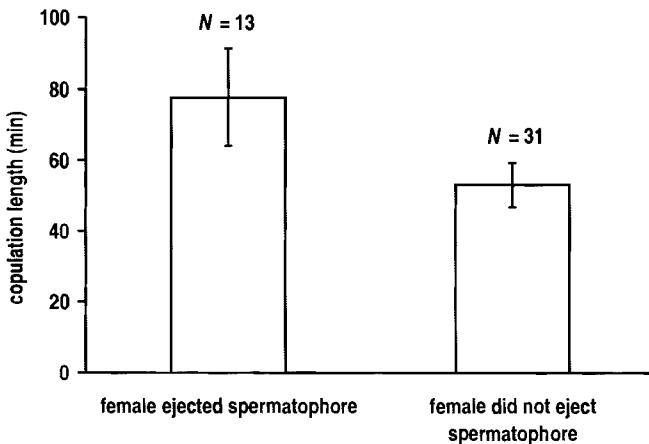


Fig. 4. *O. baranowskii* females ejected spermatophores after significantly longer copulations ($P = 0.04$).

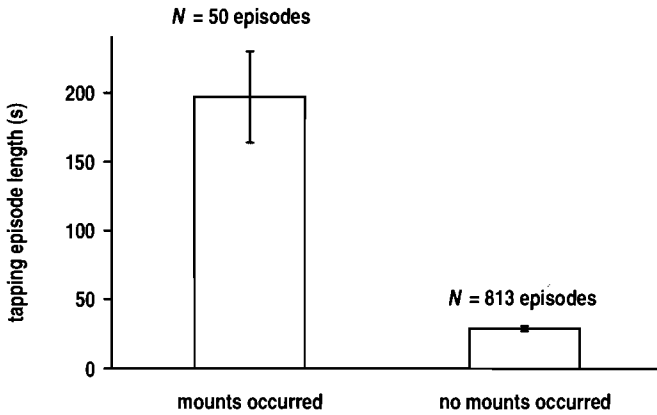


Fig. 5. *O. baranowskii* male mounts occurred during significantly longer female tapping episodes ($P < 0.0001$).

COPULATION LENGTH AND FEMALE BEHAVIOR: In *O. baranowskii* tapping incidence was negatively correlated with copulation length (Fig. 6), not so in *O. maculata* ($r_s = -0.07$, $n = 11$, $P \gg 0.50$). Copulations ended during tapping significantly more frequently in *O. baranowskii* (42 of 46 copulations) than during pushing in *O. maculata* (6 of 11 copulations, $G^2 = 7.37$, d.f. = 1, $P < 0.01$). Neither copulation length nor the incidences of tapping or pushing were correlated significantly with the incidences of the male movements or of genitalia withdrawals in either species (in all cases $r_s < 0.50$, $P > 0.10$).

COPULATIONS OF *O. BARANOWSKII* VIRGIN AND NON-VIRGIN FEMALES: Significantly more attempts resulted in copulation with virgin females (27 copulations in 35 attempts) than with females that had mated before in the lab (13 copulations in 36 at-

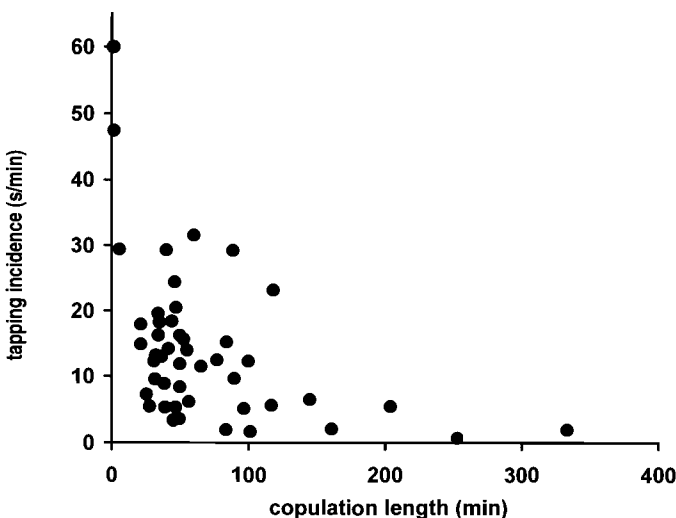


Fig. 6. In *O. baranowskii* the incidence per copulation of female tapping was inversely correlated with copulation length ($r_s = -0.52$, $n = 50$, $P < 0.001$).

tempts, $\chi^2 = 12.14$, d.f. = 1, $P < 0.005$). But when copulations of virgin females ($n = 27$) were compared with copulations of females that had mated before ($n = 13$), there were no significant differences in copulation length, the incidences of male and female movements or of genitalia withdrawals, or in spermatophore ejection (in all cases $P > 0.10$)

Discussion

Male copulatory behavior of *O. baranowskii* and *O. maculata* fits the criteria to be considered courtship (Eberhard, 1994). It was stereotyped and repeated within and between copulations, appropriate to stimulate the female and mechanically irrelevant for the male to remain coupled to the female. The hypothesis that male copulatory courtship functions to affect cryptic female choice predicts it should often differ between closely related species because of rapid evolution due to sexual selection (Eberhard, 1991, 1994). This prediction has been met in all 27 genera for which data are available (Simpson, 1975; Cowan, 1986; Eberhard, 1992, 1993a, b, 1994, 1996; Fielding and Knisley, 1995; Lachmann, 1997; Rodríguez, 1994; Rodríguez S. and Eberhard, 1994; Rodríguez S., 1998a). Male copulatory courtship differed between both *Ozophora* species in several ways: 1) leg vibration in *O. maculata* was stronger, more frequent and had a higher incidence per copulation; 2) leg vibration episodes were longer in *O. baranowskii*; and 3) the incidence of wing tapping was higher in *O. baranowskii*. Also, *O. maculata* copulations were longer and the male genitalia were withdrawn more frequently and for longer periods.

The female movement of touching the male during copulation also differed between both species: 1) in *O. baranowskii* it was a soft tapping and the hind legs moved alternately, in *O. maculata* it was a push delivered with both hind legs together; 2) episodes were longer and the incidence higher in *O. baranowskii*; and 3) *O. baranowskii* tapping was more frequent and had a higher incidence at the beginning of copulation.

Pushing in *O. maculata* seemed a direct attempt to repel the male, but its incidence was not correlated with copulation length and only one mating ended during pushing. On the other hand, the soft tapping of *O. baranowskii* was inversely correlated with copulation length and matings frequently ended during tapping. Also, short copulations that failed to result in sperm transfer had very high tapping incidences (Rodríguez S., 1998b). Taking this into account, plus the fact that tapping would fit the criteria used to evaluate male movements as courtship, the differences between the two species, and the wide variation in tapping incidence (Table 1), it seems that *O. baranowskii* tapping may function in female choice during copulation. Applied selectively, tapping may "tire" the males, possibly inducing them to release the hold of their parameres on the ovipositor. Several trends are in accord with this hypothesis: male mounts occurred very frequently during tapping, especially during the second half of episodes and especially during long episodes. Mounts may reduce the impact of tapping by taking the male out of the range of the movement.

Alternatively, tapping might inform the male about the female's willingness to accept his sperm, use it to fertilize her eggs, etc. An example occurred in the midge *Culicoides melleus* (Linley and Adams, 1972; Linley, 1975a, b; Linley and Hinds, 1975a, b; Linley and Mook, 1975). Experiments showed that the stylized kicks female *C. melleus* deliver to the male during mating induce him, not by force but as a signal, to release his hold on her genitalia. Early termination of copulation decreased

the amount of sperm transferred to the spermatophore and the likelihood that it would remain attached to the female after copulation, thus shortening unwanted matings for the female and saving the male's sperm for other females.

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