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MATE CHOICE IN GROUND CRICKETS (GRYLLIDAE: NEMBOIINAE)

T. G. FORREST
National Center for Physical Acoustics
University of Mississippi
University, MS 38677

J. L. SYLVESTER, JR., SAM TESTA III, STEPHANIE W. SMITH, ANDREA DINEP,
TANYA L. CUPIT, J.M. HUGGINS, KATHRYN L. ATKINS, MICKY EUBANKS
Dept. of Biology
University of Mississippi
University, MS 38677

ABSTRACT

To infer mating preferences of female *Neonemobius* sp., we monitored their proximity to males paired in laboratory enclosures. Females were found significantly more often near the larger of the males, and more often near a calling male than a silent one. The proportion of time individual males were observed calling was significantly correlated with male size. Females did not prefer virgin to mated males. When allowed to mate, females mated with the larger of the pair 5 of 7 times. Female preference for large males may result from selection on females to obtain larger investments from males. Female nemobiine crickets feed on glandular secretions provided by males during mating. Large males may offer more material, and females may use male calling songs as a cue to male size.

RESUMEN

Para inferir la preferencia copulatoria de hembras de *Neonemobius* sp., chequeamos su proximidad a machos apareados en jaulas en el laboratorio. Las hembras se encontraron significativamente más a menudo cerca de los machos más grande, y más cerca del macho que llamaba que del silencioso. La proporción del tiempo que se observó a los machos llamando estuvo significativamente correlacionado con el tamaño del macho. Las hembras no prefirieron a machos vírgenes sobre aquellos que habían copulado. Cuando se les permitió copular, las hembras copularon con el más grande de la pareja en 5 de 7 veces. La preferencia de las hembras por machos grandes pudiera ser por la selección de hembras para obtener mayores inversiones de los machos. Grillos hembras de nemobiine se alimentan de segregaciones glandulares proveídas por machos durante la copulación. Los machos más grande pudieran ofrecer más material, y las hembras pudieran usar los cantos llamativos como una pista del tamaño del macho.

Mating in many insects involves nuptial feeding by the female (Thornhill 1976, Thornhill & Alcock 1983). In crickets nuptial feeding may take many forms. Although not generally considered nuptial feeding, female crickets usually eat the spermatophores produced by their mate, and in some species this may be a considerable number (17 in a single mating, *Orocharis luteolira*, T. G. Forrest personal observation). In *Grylloides supplicans*, a proteinaceous spermatophylax accompanies the spermatophore and is eaten by the female (Sakaluk 1984). In some species, females feed on glandular secretions produced by the male (eg. *Oecanthus* spp., Walker & Gurney 1967), or on male body parts (eg. *Hapithus agitator*, Alexander & Otte 1967). Courtship feeding may function to delay spermatophore removal before the sperm have emptied from the ampulla into the female's spermatheca (Sakaluk 1984). Materials eaten by females may be incorporated into eggs and increase female fecundity (Gwynne 1984). Sakaluk & Cade (1980, 1983) showed that female *Gryllus integer* and *Acheta domesticus* that mated repeatedly produced more offspring than those allowed only a single mating.

Mate choice in field crickets (Gryllinae) has received much attention because males usually offer little more than sperm to mates. Thus, this system offers a means to examine female choice of males that differ in their genetic, rather than material, contribution to offspring. *Gryllus* females have been shown to prefer larger males (*G. bimaculatus*, Simmons 1988) and older males (*G. veletis* and *G. pennsylvanicus*, Zuk 1987). Differences in the calling song of male crickets are used by females in making the discrimination (Crankshaw 1979, Hedrick 1986, Simmons 1988, Zuk 1987).

During copulation, female ground crickets (Nemobiinae) feed on the proximal tibial spur of the male's hind leg and eat the glandular material that exudes from the wound (Mays 1971). If investment by males increases the fitness of females, selection should act on female behavior to increase the investment they obtain from males. For instance, if male size is a direct indicator of the amount of his investment, females should mate preferentially with larger males (Gwynne 1982, Bailey et al. 1990).

We used a paired choice experiment to examine female choice of males differing in size. We also examined whether a male's mating history (virgin or non-virgin) or his propensity to call influenced the female's decision.

MATERIALS AND METHODS

Cricket used in the experiment were the F₁ progeny of *Neonemobius* sp. females (N = 3-8) collected 18 May 1989 at Roosevelt State Park, Scott Co., Mississippi. Offspring were reared in plastic enclosures containing 3-5 cm sand. Ground dog chow was provided ad libitum. The sexes were separated prior to adulthood and held 4-8 per enclosure. Voucher specimens have been deposited in the University of Mississippi Entomology Museum. Tape recordings of males are kept by T. G. Forrest.

Paired choice experiments were carried out in the laboratory using plastic enclosures (13 x 28 x 12 cm). The bottom of each enclosure was covered with moist sand 2.5 - 4.0 cm deep, and the enclosure was partitioned into three sections using screen wire. The middle section was further subdivided into three equal areas using cardboard partitions (A, B, and C; Fig. 1).

Prior to the experiment, we estimated male sizes by measuring their mass to the nearest 0.1 mg using a Sartor model AR1014 balance. Eighteen males were ranked relative to mass. Males were paired to keep the same relative size difference between the larger and the smaller of the pairs. Large males were paired with medium, and medium-sized males paired with smaller males (see paired symbols, Fig. 2).

Males from each pair were randomly assigned to the outer sections of an enclosure (male A and B; Fig. 1). A virgin female was placed in the central section of the enclosure. The screen wire partitions allowed the female to see the males and hear their calling

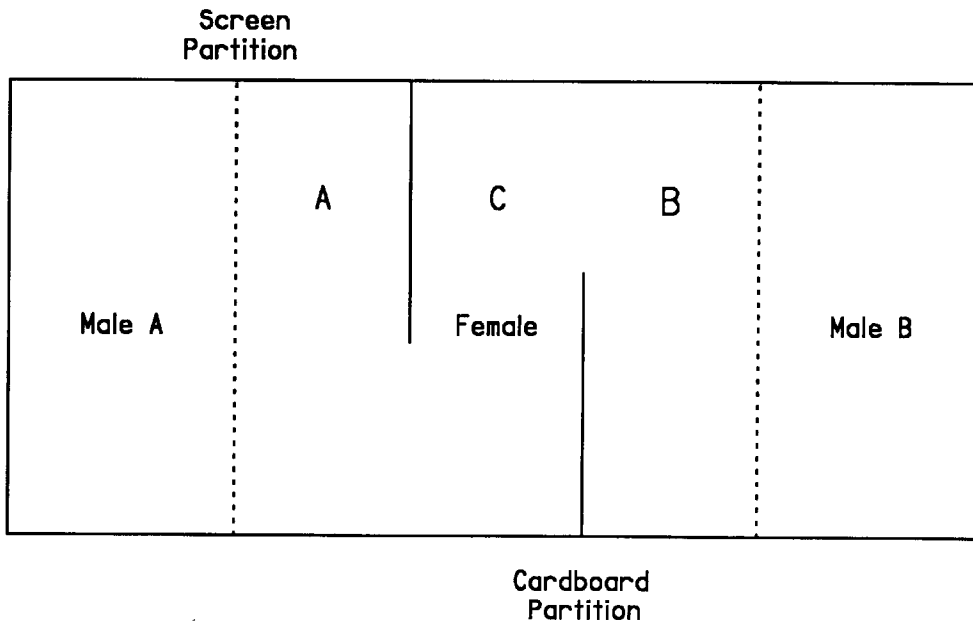


Fig. 1. Enclosure used in paired choice experiments. Males of different sizes were randomly assigned to an end section (Male A, Male B). Screen partitions allowed females in the central section to hear and see males. Cardboard partitions divided the female's section into three equal areas and prevented her from seeing both males at the same time. Female position (area A, B or C) and whether males were calling were scored during each observation.

songs. However, the cardboard partitions kept the female from viewing more than one male at a time. A 2.5 cm strip of plastic tape placed along the sides and top edge of the screen partitions prevented crickets from climbing over the screen partitions. We provided ground dog chow for each cricket in small plastic dishes. The female's food was located in the center of the enclosure. There were nine replicates.

Each day we made three observations separated by two or more hours (between 0730-0930, 1130-1330 and 1530-1730 hours). During each observation we noted the location of the female with respect to the three areas in her section (near male A, male B or Center; Fig. 1). We also noted whether the males were calling. Because males often stopped stridulating when the enclosure was approached, a male was considered calling if his wings were raised in the characteristic calling position.

During the first week, both males in the enclosure were virgin with intact tibial spurs. After the first observation on the sixth day of the experiment all partitions were removed. The following day (about 30 hours), the males were removed, weighed and checked to see if mating had occurred (i.e. tibial spurs were damaged). The experiment was repeated for a second week using the same males (one dead male was replaced) and new, virgin females. The difference in mass between paired males ranged from 1.6-6.1 (beginning of first week) and from 0.6-9.3 mg (beginning of second week).

Statistical comparisons were made using Wilcoxon's signed rank test for paired observations (Sokal & Rohlf 1981). In comparisons involving female choice, the number of observations of a female positioned near small (or virgin) males was compared to the number near large (or mated) males. For male calling, the comparisons were between the number of times small and large paired males were observed calling. Simple product-moment correlation between male mass at the beginning of the experiment (size) and the proportion of observations (square root transformed) males were found calling was

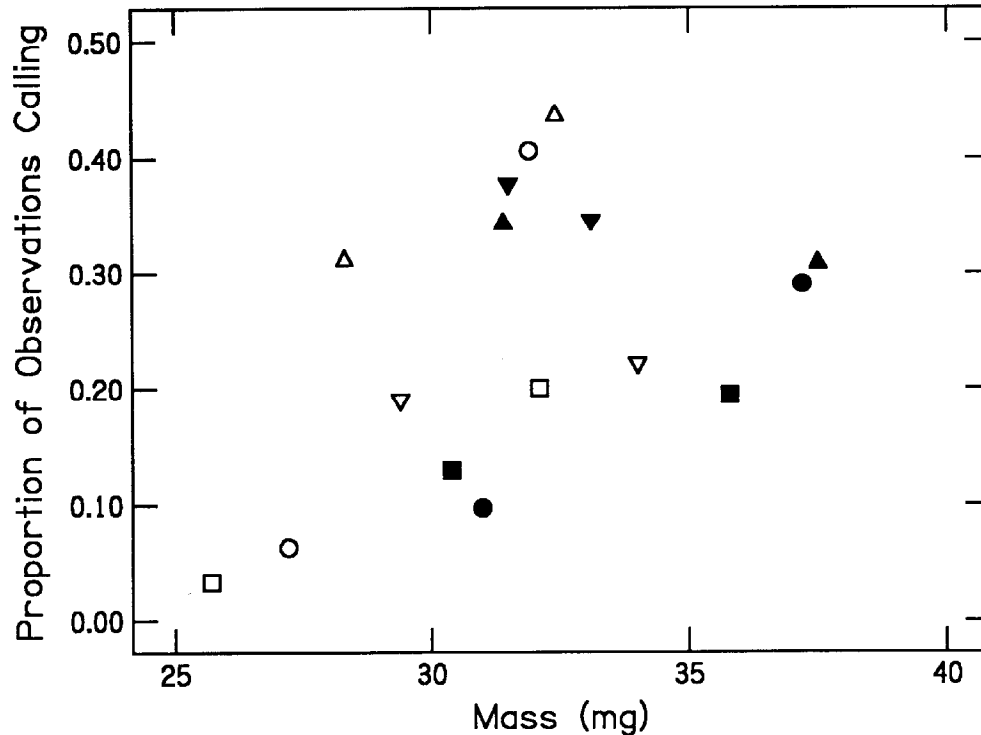


Fig. 2. Relationship between mass of individual males at the beginning of the experiment (week I) and the proportion of observations ($n=29-31$) each was found calling. Each point represents data from one individual. Data points with the same symbol show data from males paired during the experiment. Correlation between mass and proportion of observations calling (square root transformed) is significant ($r=0.53$, $p<0.05$).

calculated (Sokal & Rohlf 1981). During both weeks in one enclosure, one male of the pair died; data on female choice after the death of the males and calling data for males in this replicate were not used in any of the analyses. Female choice data from another replicate during the second week were discarded because the female was a last instar juvenile.

RESULTS

We made 247 observations of female positions during the two week period. In paired choice comparisons, the 17 females were significantly more likely to be found near the large male ($N=17$, $T_s=19.5$, $P<0.005$; week I: $N=9$, $T_s=6$, $p<0.03$; week II: $N=8$, $T_s=9$, NS). When only one of the two males was calling and the females were closer to one of them, they were found near the calling male more often (59 of 71 observations). When both males were calling and the female was near one of them, she was more likely to be next to the large male (15 of 20 observations).

At the end of the first week, four females mated with large males, one mated with a small male, one mated with both males. During the entire experiment, when females mated with only one male of the pair, the larger male was chosen 5 of 7 times. There was no significant difference between female proximity to virgin or non-virgin males during the second week of the experiment ($N=5$, $T_s=6$, NS).

During the two week period, large males were observed calling significantly more often than the smaller males paired with them ($N=8$, $T_s=4$, $p<0.03$). There was a

significant correlation between male size and the proportion of observations males called ($r=0.53$, $p<0.05$, Fig. 2).

DISCUSSION

Male size and calling influenced the positions of females in our experiment. Females can apparently judge male size without contact and may use the calling song as the cue. We did not measure the sound output of the males in the experiment. However, calling song intensity has been shown to be directly related to male size in a number of orthopteran species (*Scapteriscus acletus* and *S. vicinus*, Forrest 1983; *Anurogryllus arboreus*, Walker 1983a; *Mygalopsis marki*, Bailey and Thiele 1983, *Gryllus bimaculatus*, Simons 1988), and females often respond preferentially to louder songs (*Gryllus integer*, Cade 1979; *Scapteriscus acletus* and *S. vicinus*, Forrest 1983, Forrest & Green 1991; *Conocephalus upoluensis* and *Requena verticalis*, Bailey 1985).

In our study females also mated with large males more often than smaller males (5 of 7). Whether this preference occurs in natural populations of ground crickets has not been examined. In nature, about 80 percent of the males have their tibial spurs damaged (i.e. are mated, Mays 1971). Five males collected from Roosevelt St. Park late in the season (15 Oct 1989) ranged in weight from 21.3 - 36.6 mg. Only one of them did not have both spurs chewed; it was the smallest male. Whether the differences in male mating success can be attributed to female choice or passive attraction depends on whether females use a decision rule in choosing mates (Parker 1982, 1983). If females prefer males that call over males that remain silent, as suggested by our data, then differences are due to female choice.

What benefit female ground crickets gain from mating with larger males is unknown. Larger males might provide a larger nuptial offering. In katydids, a male's spermatophylax may be 2-20 percent of his body weight (Gwynne 1983). Female *Conocephalus nigropleurum* always mate with a larger male when given a choice, presumably to obtain a larger investment from the male (Gwynne 1982). Gwynne (1988) has also shown that nutrients from the spermatophylax are incorporated into eggs fertilized by the investing male, and that the investment may increase the number and size of the eggs produced (Gwynne 1984).

Interestingly, the juvenile female's data that were discarded from the analysis were similar to those of adults. She was found near the larger male on 13 of 15 observations, but did not (or was not allowed to) mate with either of the males. Fulton (1915) observed an immature female feeding on the metanotal gland of an adult male *Oecanthus*. Immature nemobiine females may respond to adult males and attempt to obtain nuptial food without mating. Bell (1980) found *Oecanthus* females often engaged in such opportunistic feeding, consuming the glandular secretions of males while they interacted with recent mates.

Nuptial feeding may also prevent females from removing the spermatophore before the sperm have emptied (Sakaluk 1984). In another nemobiine, *Allonemobius fasciatus*, females terminate copulation earlier if the male's tibial spurs are covered and she is unable to feed on the glandular material (Bidochka & Snedden 1985). However, the duration of spermatophore attachment did not differ between females that were allowed to feed on the spur and those that were not (Bidochka & Snedden 1985).

Time and duration of calling by male crickets are often variable (Walker 1983b), and have been shown to have an underlying genetic component (Cade 1981, Hedrick 1988). We observed large male ground crickets calling significantly more often than small males paired with them, and there was a significant correlation between male size and the proportion of time observed calling (Fig. 2). Calling behavior may be conditionally dependent on size or the presence of other males. Large males might have more energy

to invest in sound production and call to advertise their 'vigor' (Burk 1989, Ryan 1989). Small males may call less often when caged with another male, because in nature this would encourage aggressive interaction from other, larger males (Burk 1983). One possible reason for the low correlation between a male's mass and amount of calling (Fig. 2) is that medium-sized crickets may call differently when competing with smaller males compared to when paired with males of similar or larger size. Small males may be predisposed to become silent, satellite males (Cade 1979).

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