

# MATING BEHAVIOR OF *NEOCONOCEPHALUS ENSIGER* (ORTHOPTERA: TETTIGONIIDAE) WITH NOTES ON THE CALLING SONG

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## Abstract

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*Neoconocephalus ensiger* (Harris) mating is described from field observations. The sequence of mating events is presented along with a brief description of the physical parameters of the calling song. Mating differs from other tettigoniids in that the copulation time is longer and there is no external evidence of a spermatophore. The significance of these differences is discussed.

## Introduction

The calling song of *Neoconocephalus ensiger* (Harris) is one of the commonest summer evening sounds in southern Ontario. Pierce (1948) and Borror (1954) described the physical parameters of the song, while Frings and Frings (1957) demonstrated how chirp rate is affected by temperature. More recently Walker (1975) has shown the surprisingly complex relationship between wing movements and the sound produced during calling in *Neoconocephalus*.

The reproductive behavior of several species of Tettigoniidae has been investigated; however, most of these studies have been limited to pair formation, especially the functional analysis of calling song parameters (e.g. Baier 1930, Busnel and Dumortier 1954, Spooner 1964, 1968, Bailey and Robinson 1971, Morris *et al.* 1975). Only a few studies have investigated later stages of tettigoniid mating (e.g. Boldyrev 1914, Leroy 1969, Rentz 1972). *Neoconocephalus* has been better studied than most other genera in this regard; Boldyrev (1914) described copulation in *N. nitidulus* (Scopoli) and Whitesell, in an unpublished thesis (1969), reported observations on single copulations of *N. retusus* (Scudder) and *N. triops* (L.). The present paper described the mating behavior of *N. ensiger* from pair formation to the final separation of the male and female.

## Materials and Methods

Immature females of *N. ensiger* were collected from localities near Brampton, Ont., during June and July 1974. They were reared to adulthood in large communal cages in the laboratory. As each female matured she was removed from the cage and housed in a numbered glass cylinder, approximately 9 cm high and 9 cm in diameter, covered at both ends with fiberglass screen. All females were fed on horsemeat, apple, barley seedlings, and assorted seeds.

Calling songs of *N. ensiger* males were recorded at 19 cm/sec on a Uher 4000 Report L tape recorder and behavioral observations were read into a Phillips cassette recorder. All observations were made in red light from a headlamp. Oscillograms of time-amplitude patterns were made with a Tektronix oscilloscope (model 564) and an oscilloscope camera. A Tektronic frequency analyzer plug in unit (type 345) was used to obtain frequency spectrograms and a Sonograph 7029A was used to make audiospectrograms.

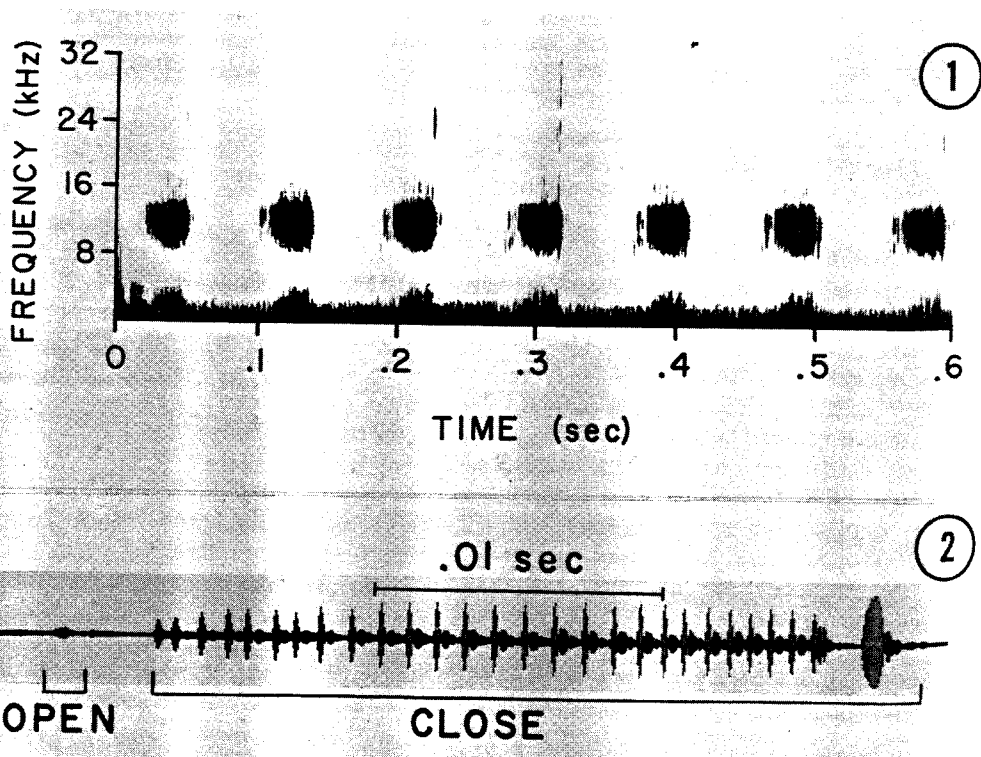
The protocol for mating behavior observations was as follows: in the field a Uher microphone, attached to the end of a 1 m ski pole, was positioned approximately 20 to 30 cm from a singing male. A portion of the male's calling song was recorded, then the female was released from her housing jar. Recording of male sounds was stopped as

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soon as they were in copula. After the pair had separated, post-copulatory behavior was observed for about 10 min. Most katydid were recaptured after the observation period and voucher specimens were placed in the Royal Ontario Museum, Toronto. Five complete matings were observed.

### Observations

**Calling song.** The calling song consists of a wide band of frequencies with the most intense lying between 8 and 17 kHz (Fig. 1). This agrees with the range given by Borror (1954). The main energy measured is from 11 to 12 kHz which is less than the 13.7 kHz determined by Pierce (1948). Pulse trains are produced at a rate slower than most other *Neoconocephalus* species (Walker 1975), about 6/sec at 15°C (Frings and Frings 1957) (the calling song in Fig. 1 is at a higher rate, about 10 pulse trains/sec at 15°C). Walker showed that the opening of the tegmina is nearly silent with "an acoustically effective closure" generating the pulse train. The present observations are similar to Walker's, that the pulse train is a series of rapid decay pulses; however, the train ends with an intense prolonged pulse which was not obvious until the song was sufficiently slowed (Fig. 2). Walker stated that the last half of the file is traversed with the tegmina "snapping quickly and nearly silently shut" and that this movement has no obvious function. This last part of the closure seems a likely candidate as the movement which produces the final grylloid pulse; the snapping action of the wings driving the scraper over the file. Dr. Walker (letter 1975) has reanalyzed his films of *N. ensiger* calling and is now convinced that the rapid tegminal movement does produce a sound.



FIGS. 1-2. 1, audiospectrogram of *N. ensiger* calling song at 15°C; 2, oscillogram of a single pulse train showing sounds corresponding to the opening and closing of the tegmina as described by Walker (1975).

**Mating behavior.** Males of *N. ensiger* start to sing at dusk and usually call from grass stems, oriented upward, about 50–70 cm above the ground. When a sexually responsive female is released near a calling male she moves immediately toward him by walking and occasionally flying. Usually the female does not go directly to the male; she moves vertically in the vegetation closeby, this movement possibly functioning in localizing the sound source. Eventually the female reaches the same stem as the male and moves toward him. Apparently at this point the male detects the female and will orient toward her, often moving a few centimeters in her direction. The pair then move together and antennate each other. Copulation ensues quickly as the pair move past each other on the grass stem, the male arches his abdomen and they engage genitalia. The male usually continues to stridulate until they come into physical contact, at this point the male's song becomes sporadic and stridulation stops as soon as they are in copula. When the pair comes together there appears to be no change in song other than this brief sporadic termination. Comparison of the time–amplitude patterns of a single male's calling song, before contacting the female, with the last sounds he made before copulation revealed no obvious differences in pulse train rate or structure of individual pulse trains.

The copulating pair is invariably positioned on the plant stem so that the male faces down and the female faces upward. If the female approaches the male from above the pair turns so that the male still faces downward ( $N = 2$ ) (Fig. 3). Both male and female use the tarsi of the first two pairs of legs to grasp each other's tegmina and the supporting vegetation (the male often grasps the ovipositor of the female). Their extended metathoracic legs are held away from their bodies above the tegmina. The only continuous movements occurring while the pair are in copula are antennal movements, mainly by the female. During the first few minutes of copulation the male exhibits rhythmic movements of his subgenital plate against the base of the female's ovipositor, accompanied by pumping movements of his abdomen. Alexander and Otte (1967) refer to these movements in orthopteran copulation as "probably aiding in proper positioning and engagement of genitalic parts," although they are probably also involved in spermatophore passage. Quivering of the pair was observed during early copulation and the male often quivered during the later stages of copulation, in one case just after the pair had separated. Duration of copulation ranged from 27 to 68 min ( $N = 5$ ,  $\bar{X} = 40$  min); usually the female initiated separation by moving her legs and pushing away from the male. In no case was a spermatophore observed to be attached to the genitalia of the female after the pair had separated.

After separation they move apart and within 3 min the male stops, bends his abdomen between his legs and grooms his genitalia. Although Whitesell (1969) observed post-copulatory genitalia grooming in both sexes of *N. triops* and *N. retusus*, *N. ensiger* females were never observed to groom their genitalia.

In three out of five matings observed, the males resumed calling shortly (from 10 sec to 8.5 min) after copulation but the female was never reattracted to calling during the 10 min following copulation.

### Discussion

Pair formation in *N. ensiger* is achieved by the attraction of the sexually responsive female to the calling male. This is the method of pair formation most often observed in the Tettigoniidae, Gryllidae, and Cicadidae, the "singing insects" (Alexander 1967).

When the female arrives near the male, the displacement of the plant from which he is calling seems to be the stimulus for him to orient toward her. *N. ensiger* was never observed to actively shake the plant as Whitesell (1969) has recorded for *N. retusus*. The *N. retusus* female which he observed started to shake when she landed near the male, who stopped stridulating and also shook his body. Males of *N. ensiger* continued

to stridulate until making physical contact with the female. According to Busnel *et al.* (1955) body-shaking by an individual of *Ephippiger* sp. signals its presence to the opposite sex. Like *N. reusus*, a male *Ephippiger* starts to shake when the plant from which he is calling is agitated. Recently Alexander (1975) has suggested a selective

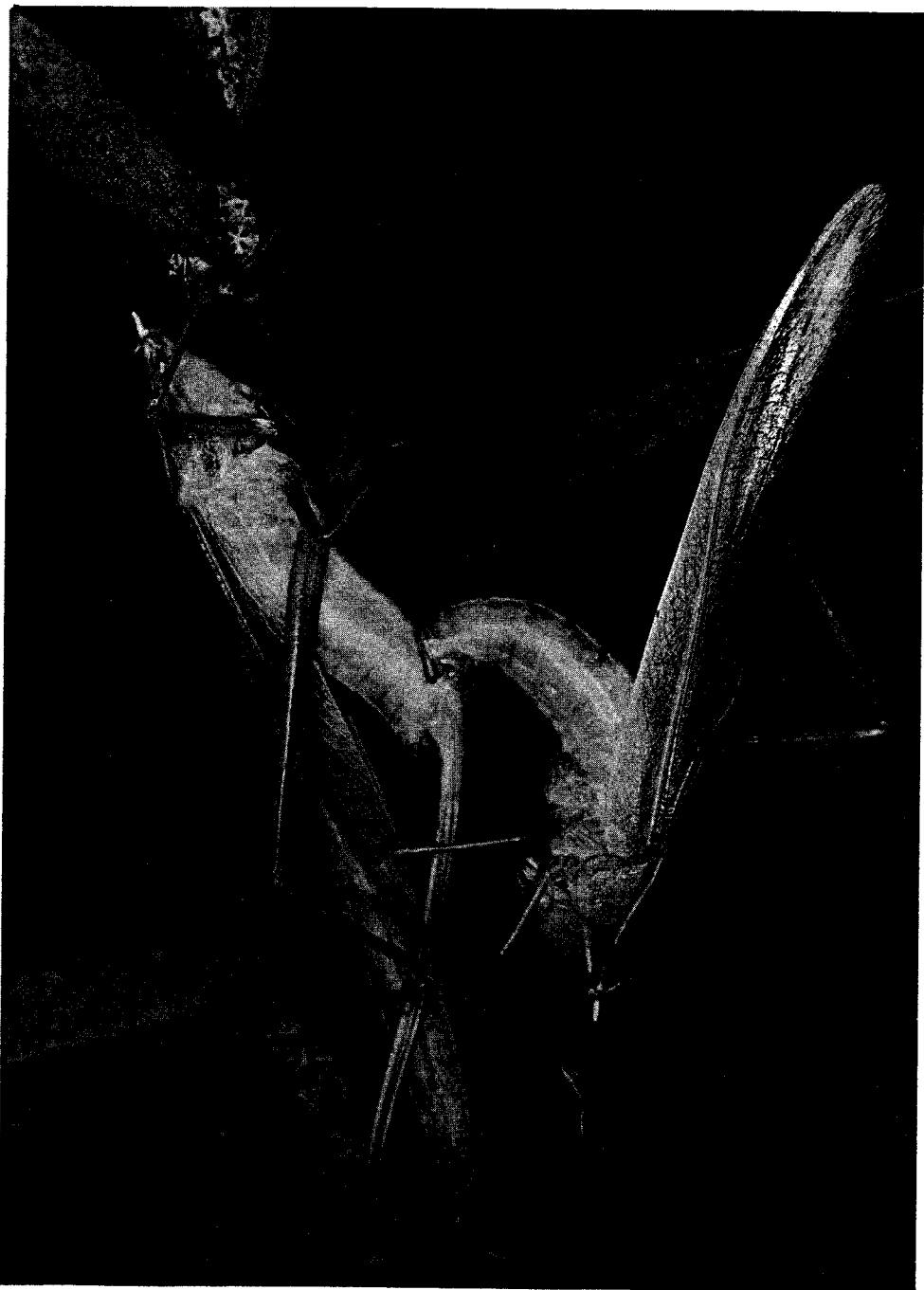


FIG. 3. A copulating pair of *N. ensiger*.

advantage of the change from stridulation to shaking, when the male's perch is agitated. Shaking is a "less risky channel" when the chances of cuckoldry are high, in that it is potentially transmissible to the responding female but not to nearby males. Also it could function as an aggressive signal if the insect agitating the plant is another male (Alexander 1975). The difference in the pre-copulatory behavior of *N. ensiger* and *N. retusus* could indicate that cuckoldry is more likely in the latter species. Male quivering, exhibited during copulation, could also be an aggressive signal functioning in keeping other males from interfering with the copulating pair.

The position assumed during copulation (Fig. 3) is the second of three kinds of copulatory positions described by Alexander and Otte (1967). This "end to end" position, unlike certain other tettigoniids, does not follow an initial "female above" position. Some burrowing Gryllidae and Gryllacrididae also exhibit end to end copulation. Alexander and Otte consider grass stems and burrows to place similar restrictions on movement during mating and thus selection could have limited both burrow and grass dwelling orthopterans to this position.

The absence of an observable spermatophore has been noted in other *Neoconocephalus* species and is in contrast to most other tettigoniids; the spermatophore appears to be mostly internal. Boldyrev (1914) gives a figure outlining the position of the internal spermatophore in the genital tract of a female *N. nitidulus*. Also, Dr. T. J. Walker (pers. comm.) observed this in *N. retusus* and has mentioned that one of the possible advantages of this system is that the spermatophore could act as a "mating plug." Two main evolutionary advantages of copulatory plugs were given by Parker (1970): one, it assists insemination by preventing loss of semen from the female and secondly, it reduces the chances of further insemination by other males. A disadvantage of the system, however, is that the internal spermatophore in *Neoconocephalus* seems to necessitate a longer copulation time than many tettigoniids (the copulating pair being more vulnerable to predation) (T. J. Walker, pers. comm.). The duration of copulation in *N. retusus*, which Whitesell (1969) reported, was 40 min ( $N = 1$ ) which is equal to the mean copulation time of *N. ensiger* ( $N = 5$ ). Many katydids have extremely short copulation intervals. Leroy (1969) recorded copulation times from  $\frac{1}{2}$  min. to several minutes for three species of Trinidad Phaneropterinae which have external spermatophores.

After copulation the male tettigoniid is usually unable to produce another spermatophore for a very long time (Alexander 1961). Also, according to Huber (1955), calling in crickets is not resumed after copulation until a new spermatophore is produced. Dumortier (1963) reported that *Ephippiger* males do not resume their calling songs until 3 to 5 days after mating. Body weight in males, observed before and after copulation, showed that the spermatophore produced is about 25% of the male's total weight. *N. ensiger* males start to call within a few minutes of separation from the female so presumably the males are ready to mate again soon after copulation; the formation of a spermatophore appears to be less physiologically taxing in this species. During the long copulation of *N. ensiger* a new spermatophore could be formed while the old one is positioned in the female's genital tract.

A recent paper by Thornhill (1976) discusses how a male insect may increase his investment in his offspring by increasing the nutrition to the offspring. Thornhill suggests that this can be achieved indirectly by feeding the female. He further states that a large spermatophore, which the female consumes, may be significant as a nutrient. The spermatophylax (after Boldyrev 1914) is a sticky matrix which is an integral part of the tettigoniid spermatophore. The spermatophylax of species with external spermatophores is commonly very large and is consumed by the female after copulation (e.g. Rentz 1972). Thus two male reproductive strategies appear to be present in the Tettigoniidae: (1) as exemplified by *Ephippiger*, to produce fewer spermatophores, each

with a large spermatophylax, and invest more in fewer offspring and (2) as in *Neoconocephalus*, to produce many small spermatophores resulting in a greater number of offspring but with less paternal investment in individuals.

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