

MATING BEHAVIOR OF NEMOBIINE CRICKETS—
HYGRONEMOBIUS, *NEMOBIUS*, AND *PTERONEMOBIUS*
(ORTHOPTERA: GRYLLIDAE)¹

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ABSTRACT

Pteronemobius females mount and briefly couple genitalia with males that have not yet formed spermatophores. This preliminary mounting, previously unreported for *Pteronemobius* and unique among Gryllidae, is prerequisite for spermatophore production in each mating sequence. The female mounts and couples genitalia with the male a second time and receives the spermatophore. The two remain coupled for an extended period while the female feeds on specialized tibial spurs of the male. This sequence is basically the same for 10 species in 3 subgenera as follows: (*Allonemobius*) *ambitosus* species complex 3 spp., *fasciatus*, *sparsalsus*; (*Neonemobius*) *cubensis*, nr. *mormonius* Florida, nr. *mormonius* So. California; (*Eunemobius*) *carolinus*, *melodius*. The mating pattern of *Pteronemobius* is interpreted as derivative from one like *Nemobius sylvestris* where males form and pass a small spermatophore prior to a much larger one. After each spermatophore is passed the female often feeds on a glandular area at the base of the male's tegmen. Mating in *Hygronemobius alleni* is no more complex than in most other gryllids: courtship is brief, a full-sized spermatophore is passed during the first mounting, and behavior after spermatophore tube insertion involves no mouthing of special glandular areas and no continued coupling.

In most crickets the female mounts the male prior to copulation. A spermatophore that is formed before this mounting is generally visible at the end of the male's abdomen. The tubular process of the spermatophore is inserted into the female but the spermatophore itself remains external. Internal pressures, developed by diffusion of fluid across a semi-permeable membrane within the spermatophore, force sperm through the tube into the female (Khalifa 1949).

In some species, the female feeds at a specialized glandular area of the male following receipt of the spermatophore. The most elaborate of such areas are the metanotal glands, found in all species of Oecanthinae, some Eneopterinae and a few Gryllinae (Walker and Gurney 1967). Only members of the nemobiine genus *Pteronemobius* have a special glandular spur on the male's hind tibia (Fulton 1931), while a closely related European genus, *Nemobius*, has an apparently glandular area at the base of the right tegmen. Alexander and Otte (1967) discussed mating in *Pteronemobius* and *Nemobius* by comparing Fulton's (1931) and Gabbutt's (1954) observations with their own observations of *N. sylvestris* and *P. allardi*. Descriptions of mating of *N. sylvestris* by Richards (1952) and Gabbutt (1954) appeared the most detailed and complete but because of their complexity were difficult for Alexander and Otte (1967) to relate to mating in *Pteronemobius*. The present study reveals undetected complexity in *Pteronemobius* that simplifies this comparison. *Hygronemobius alleni*, the sole United States representative and type of this large Neotropical genus was

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TABLE 1. LOCALITY, NUMBER OF OBSERVATIONS, AND LIGHTING FOR STUDY OF MATING IN 11 SPECIES OF NEMOBIINAE.

Species	Locality	Number of Matings Observed	Light** Conditions
<i>Pteronemobius</i> (<i>Allonemobius</i>)*			
nr. <i>ambitosus</i> 531 B	North-Central Fla.	20†	On
nr. <i>ambitosus</i> 531 D			
nr. <i>ambitosus</i> 528			
<i>fasciatus</i>	Gainesville, Fla.	2	On
<i>sparsalsus</i>	Cedar Key, Fla.	3	Off
<i>Pteronemobius</i> (<i>Neonemobius</i>)			
<i>cubensis</i>	Florida	3	Off
nr. <i>mormonius</i> 535	North & West Fla.	2	On-Off
nr. <i>mormonius</i> 527	Riverside Co., Cal.	4	On-Off
<i>Pteronemobius</i> (<i>Eunemobius</i>)			
<i>carolinus</i>	Gainesville, Fla.	2	On-Off
<i>melodius</i>	Gainesville, Fla.	2	On-Off
<i>Hygronemobius</i>			
<i>alleni</i>	Flamingo, Fla.	13	On-Off

*Vickery and Johnstone (in press) have proposed that the subgenera *Allonemobius*, *Neonemobius* and *Eunemobius* be given generic status.

**On=florescent lighting (90 ft-c) ; Off=Westinghouse red bulb (<.5 ft-c)

†All *ambitosus* combined

studied for comparison with *Nemobius* and *Pteronemobius* because it lacked external glandular areas like most other Nemobiinae.

METHODS

Representatives of all North American genera and subgenera of Nemobiinae were available for study (see Table 1 for list of species) and comparison with published accounts of mating in *Nemobius sylvestris* from Europe.

Specimens used in mating were reared by isolating single field collected females in wide mouth gallon jars containing about 2 inches of sand, a small cap of crushed dog food and a water vial. Water was added to the sand near the wick of the water vial to provide humidity and a site for oviposition. Penultimate and antepenultimate female nymphs were transferred to holding jars and reared to virgin adults. Calling songs of sibling males were recorded to verify the song type of each group of females. These males plus recorded field collected males, were mated with the reared virgin females.

Matings were observed of pairs confined in the following types of cages: (1) clear plastic or screen cylinders (4×4 inches) placed on moist sand, (2) wide mouth gallon jars containing about 2 inches of sand, (3) 4 inch² screen covered cages. The plastic or screen cylinders were used for still and motion picture photography and sound recording since once courtship began, the cylinders could be removed without disturbing the crickets.

Females walked about new containers, generally unresponsive to males immediately following transfer, whereas males began courting almost as soon as they were transferred and contacted a female. For this reason females were allowed 2 or more hr to acclimate to their new surroundings. When mating was to take place on sand, males were restricted beneath overturned 1 inch diam plastic vials in the same container with the female for the acclimation period, or they were released directly into containers with acclimated females. All observations were made in a carpeted room, lined with acoustic tile, and at $25^{\circ}\pm 2^{\circ}\text{C}$. Mating behavior studied under bright (90 ft-c) and very dim red light (7.5 ft-c) (Table 1) was similar, with the exception that occasionally movements the author made while observing, disturbed the crickets when the lights were on. The individuals observed or specimens from the same laboratory colonies are deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville. Identifications were made by Dr. Thomas J. Walker, University of Florida.

Mating of *Hygronemobius alleni*
(Fig. 1)

The following is a composite description of mating of *Hygronemobius alleni* from 4 complete mating sequences (including an analysis of 2 filmed sequences) using specimens from the original field collections of adults and nymphs and from 5 complete and 4 incomplete sequences using 6 pairs of second generation laboratory reared siblings.

When a male was allowed to move freely about the container (by removing the retaining vial) he would generally contact or be contacted by the female within 3 min. At this time most males produced a short burst of song, fencd antennae with the female, and assumed a characteristic courting position, directly behind or slightly off to one side of the female. The male's song began at the first fencing of antennae and lasted for 10

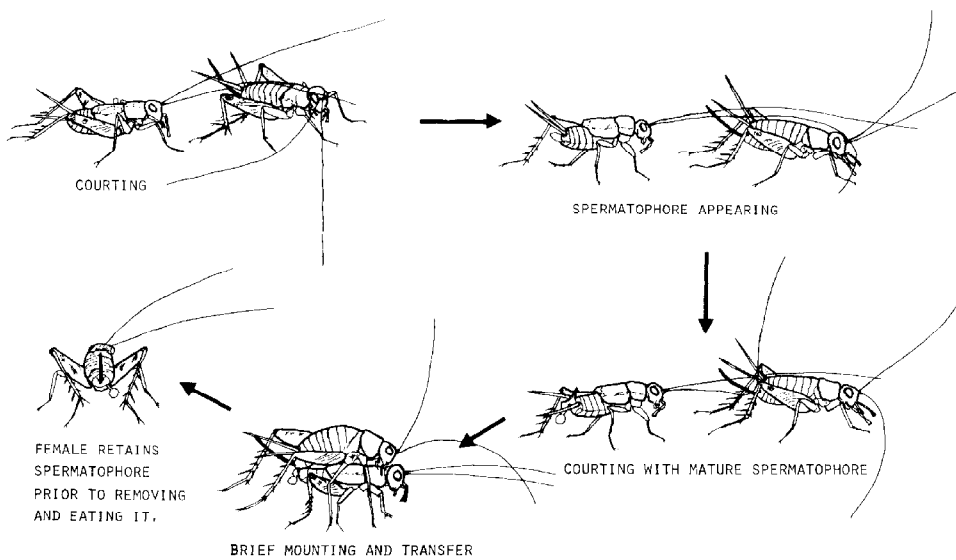


Fig. 1. Sequence of events in mating of *Hygronemobius alleni*.

sec or less. A female contacted by a male's antennae would stop, turn, and often advance toward the male as he stridulated and antennated her briefly. The male then moved behind the female and she ceased moving as he antennated her.

If the female moved from antennal range of the male, he pursued her. In one case after a 10 min chase, a male briefly walked up on a female. This male had repeatedly darted toward the female, but each time she would turn to one side and he would back off and resume antennating her.

Antennation of the female continued throughout the mating sequence and appeared to be the primary means of communication. The male lashed his antennae over the entire length of the female, particularly contacting her metathoracic legs, upturned cerci, and ovipositor. Each lash was a series of short up and down strikes of the antennae too rapid to count. Between lashings both antennae were held motionless, remaining bowed downward when contacting the female's ovipositor, cerci, or metathoracic legs, or held outward when over or lightly contacting her tegmina, thorax, head, and antennae.

The male would position himself directly behind or just to one side and antennate with an alternating left-right emphasis, giving an illusion of sweeping the antennae across the female's cerci. The ovipositor and inner margins of the cerci were frequently struck but most contact was made against the terminal portions and outer margins of the cerci, and the metathoracic legs. During a mating sequence the antennation rate (lashing episodes per min) increased (Fig. 2). The female responded to the

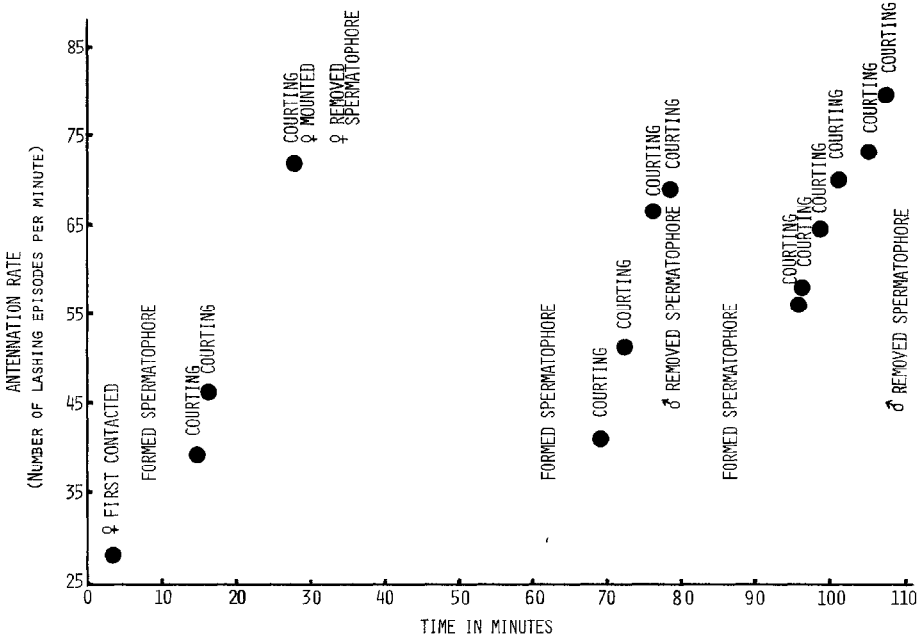


Fig. 2. Changes in antennation rate during courtship of *Hygronemobius alleni*. In the case illustrated the male completed transfer of the first spermatophore but failed with the following two.

male's antennation with a concurrent upward movement of her ovipositor and occasional rearward antennation to the male.

The spermatophore appeared 5.0, 6.0, 6.0, and 9.5 min (4 fastest sequences) after first antennal contact with the female. Holding the abdomen high, and with 5-10 pumping motions the opaque, white, pearshaped spermatophore appeared at its tip. The spermatophore was held at the distal end of the genitalia, and moved up and down as the genitalia became fully extruded. After 2 to 3 min, the spermatophore began to clear marginally, appearing as a tiny glasslike bead with a white center one-third of the total diameter. In one instance, courtship contact was loosely maintained 90 min before the spermatophore appeared, and courting continued 48 more min before the spermatophore was transferred. In situations where females appeared unresponsive and were actively walking around the cage, males occasionally removed and ate their spermatophores 15 to 30 min after formation.

The male appeared to initiate mounting 14 to 24 ($\bar{x}=18.5$, $n=6$) min after spermatophore formation by pushing forward and producing 5 to 10 soft chirps while antennating the female. In one case a male walked up to a female and palpated her cerci. She repelled him for about 3 min by slowly extending her legs backward. The male then turned around, and rocked and vibrated while stridulating in front of the female and shuffling backwards to her. When a female began to mount, the male would lower his wings. When she was directly above him he would suddenly thrust the terminal portion of his abdomen upward and transfer the spermatophore to the female. In one filmed sequence, after making an advance, a male quickly turned around in 0.11 sec (2 frames max at 18 frames/sec). Immediately the female ran up on him and coupled genitalia for 1.00 sec (18 frames) to receive the spermatophore. For most matings, the genitalia appeared to be coupled, the spermatophore transferred, and genitalia uncoupled in even less time than a second. Males bobbed their abdomens upward tapping as many as 20 times against the venter of the female before and occasionally after transfer of the spermatophore. This upward bobbing brought the male cerci into contact with the female venter and may have functioned in pair alignment. It is difficult to understand how the spermatophore tube could have been inserted into the female properly, although similar speed has been noted for *Cyrtoxipha* (Alexander and Otte 1967).

Most females (6 of 8) dismounted immediately after receipt of the spermatophore and remained motionless, as did the males, for 1 to 2 min.

Those females that did not dismount immediately remained motionless, standing upon the male. In one case, the female stood on the male for 8.5 sec. Dismounting females ran forward over the male's head or backed down the male's back. Having retained the spermatophore for 3.2 to 15.0 min ($\bar{x}=8.0$, $n=9$), females lowered their abdomens and backed up, wiping the spermatophore off against the sand. Reaching beneath themselves, females then grasped the spermatophore with their mouth parts, and spent 3.5 to 15 min ($\bar{x}=8.9$, $n=8$) consuming it. During this time the male relocated and resumed antennation of the female, frequently producing a series of 10 to 20 short chirps at 1 sec intervals usually while the female was eating the spermatophore. No other post copulatory behavior was

noted. Continued antennation by the male generally led to the beginning of another courtship sequence.

The male of 1 pair produced and transferred a sequence of 3 spermatophores with intervals of 24 and 76 min. During the hour after the third spermatophore, the male slowed and then ceased antennation of the female and walked away. Another pair coupled twice unsuccessfully, losing the first 2 spermatophores which were produced 36 min apart. A third spermatophore produced 26 min later was carried 29 min by the courting male before being removed and eaten by him. Following this, the male and female walked about the enclosure for more than 1 hr but no further courting occurred. These 2 instances suggest that a male may be able to produce only 3 spermatophores during a courtship and mating sequence.

Mating of *Nemobius sylvestris*

The following summary is taken primarily from Richards (1952, 1953) and supplemented with data from Gabbutt (1954), who apparently observed a larger number of matings. Richards wrote a description of mating as if it were a single observation, but it was likely a composite of several observations owing to the detail included.

Stridulation occurs with the first contact of a female and is accompanied by antennating and body jerking. With a "peculiar trembling gait" the male walks to relocate the female, but courts with his back toward her, yet she is not allowed to mount for 30-45 min. Gabbutt (1954) records 20 to 35 min elapsed before the female first mounts.

Just prior to the female mounting the male, the male's stridulation becomes uneven amidst violent body jerking. The female mounts the male over his lowered cerci and elytra as he pushes backwards beneath her "raising his abdomen," elevating the genital organ to the female's subgenital plate, where the spermatophore and its "fine, stalk-like tube" are transferred "instantaneously" to the female. The pair separate "at once and for a minute or so both stand motionless . . ." The male jerks backward again and the female mounts and "appears to feed on something from the male's elytra." Gabbutt described this as a resumption of male body motions and a time when the females may or may not mount and "feed" on the male's right tegmen, the whole period lasting 10 to 15 min with "feeding" occurring in only 6 of 19 cases observed. Richards' term "feeding" may better be termed mouthing since the female's labial palpa, not the mandibles are worked with a "sweeping motion" over this area. Gabbutt describes the pair separating, followed by the male pursuing the female for "as long as 15 min", followed by 5 to 15 min remaining motionless and without stridulation before a spermatophore was produced. Richards relates that this second spermatophore is "twice the size of the previous one" but Gabbutt's measurements of 0.946 mm ($\sigma_{28} = 0.016$) compared to the first 0.303 mm ($\sigma_{11} = 0.0025$) make it fully 3 times the diameter of the first.

The first spermatophore is retained by the female for 30 to 60 min before it is removed (Gabbutt). Richards notes the first spermatophore is "loosened" with the aid of spines of the female's hind tarsus before she backs over the substrate and finally rubs it off and eats it. The second spermatophore slowly "becomes translucent" around a white central core.

The male begins rapid antennation and steady stridulation while seeking the female. As before, the male courts facing away from the female, culminating in a second mating 60 to 70 min after the first. Occasionally the first and second spermatophores are carried together by a female.

Gabbutt noted "feeding movements" [mouthing] in 19 of 52 cases following transfer of the second spermatophore.

Richards doubts the receipt of the 2 spermatophores by the same female under natural conditions and even suggests "that after mating [passing the first spermatophore] the male pursues the female as if to chase her away; and, as an hour or more elapses between the 2 matings, it is more than likely that another female would normally receive the second spermatophore." However, Richards observed that when males produced a small spermatophore but were unable to mate, they would "eject" it and "devour it" and *not* produce the larger (second) spermatophore. This suggested to Richards that a preliminary sequence of events was necessary to the transfer of the larger spermatophore.

Mating in *Pteronemobius*

The genus *Pteronemobius* is unique in that males possess a proximal internal spine on each hind tibiae which is mouthed and *fed upon* by the female during a comparatively extended copulation (Fig. 2). Hebard (1913b) and Davenport (1960) recognized 3 subgenera of *Pteronemobius* for America north of Mexico. The subgenera *Allonemobius* and *Neonemobius* have unequal disto-ventral spurs on the hind caudal tibiae, the ventral margin of the ovipositor apex unarmed, and male karyotypes of 7 and 9 autosomes plus XO respectively, whereas in *Eunemobius* the spurs are equal in length, the ventral margin of the ovipositor apex is armed with minute serrulations, and the male karyotype is 3 autosomes plus XO.

Allonemobius and *Neonemobius* proved to be so similar that they are discussed here together and in contrast with *Eunemobius* from which they differ in several respects.

The Subgenera *Allonemobius* and *Neonemobius*

The following description is based primarily on observations of more than 20 mating sequences of *P. (Allonemobius) ambitiosus* (species complex), plus at least 2 complete and several incomplete sequences of the 5 other species listed in Table 1 under *Allonemobius* and *Neonemobius*.

Males respond to the first antennal contact with the female and frequently stridulate briefly while facing and antennating her. Courtship is similar throughout the mating sequences studied and is characterized by a pattern or rhythm of antennation (short bursts of rapid antennal lashing) by the male which alone appears sufficient preparation for receipt of the spermatophore by the female. The male positions himself before or just off to one side of the female and antennates her outstretched antennae. The pattern of chirps during courtship follows the pattern of antennation and is usually accompanied by a slow forward list of the body and a shift in stance without moving the legs.

Courtship songs are a series of quiet chirps. Often more widely spaced pulses begin each chirp followed by a speed up toward the end, giving the impression of an increase in pitch and intensity. One *ambitiosus* 531B

male which did not stridulate (tegmina appeared normal but physically stuck together), a male *sparsalsus*, and a male *cubensis* which stridulated very little, completed mating sequences (2 successively for the "mute" *ambitosus* 531B) with their respective females, as rapidly and as completely as those males which stridulated more during courtship.

After contacting a female, most males did not court or courted very little prior to suddenly turning around in front of her. The following backing sequence is similar for all *Allonemobius* and *Neonemobius* studied. The male trills continuously and appears to vibrate and sway back and forth in front of the female. With the first contact by the female's palpi or antennae the trilling softens in intensity, the wings are lowered some and the male begins backing beneath the female. With this lowering of the male's tegmina, a series of grating clicks and squeaks often accompanies the final wing closure. The male backs part way under the female, but simultaneously the female often walks up on the male's back. The mounting involves both sexes actively positioning themselves with respect to each other. If no contact is made by the female, the trilling increases in intensity, but the male eventually turns around and resumes courting.

Frequently the male's claspers can be seen just prior to this mounting. The claspers are apparently inserted into the female genital opening as the 2 couple together in a manner difficult to observe in detail. The pair jump and vibrate together for 1/2 to 2 sec with their genitalia firmly attached. The male is probably responsible for the jumping since he has more contact with the substrate. The pair separate in an almost violent explosion with the female bouncing upward and forward off the male's back. If the female does not mount the male in a way such that the genitalia couple, or the pair is disturbed during this phase, this process is repeated. In several instances this first mounting was repeated until the pair maintained a firm attachment of their genitalia and "jumped" together briefly without separation. This first mounting and coupling (first in a series of 2) is very brief yet it is a prerequisite for spermatophore formation and transfer. There was no instance of spermatophore formation without the male first being mounted by the female. This first mounting was repeated prior to the production of each subsequent spermatophore in all repeat matings ($n > 15$).

The male resumes courting the female following the first mounting and approximately 5 to 10 min later he forms a spermatophore. Raising his abdomen high and with a great deal of abdominal pumping, the pear-shaped spermatophore is first extruded straight backward. With additional pumping and pulsing of the abdomen, the spermatophore (carried at the proximal portion of the male's genitalia) extends downward as the genitalia are fully protruded. This extrusion of the spermatophore may or may not be accompanied by the courtship type song. Courtship continues as the male faces the female's head or side and antennates her on her outstretched antennae. Within 1 or 2 min the spermatophore becomes round and in 5 to 10 min the outer two-thirds clears.

If the female leaves the vicinity, especially after the spermatophore has been formed, the male produces a trill which appears louder than either the calling or courtship song. Generally this loud "courtship interruption" song (Alexander 1962) arrests or attracts the female, enabling the

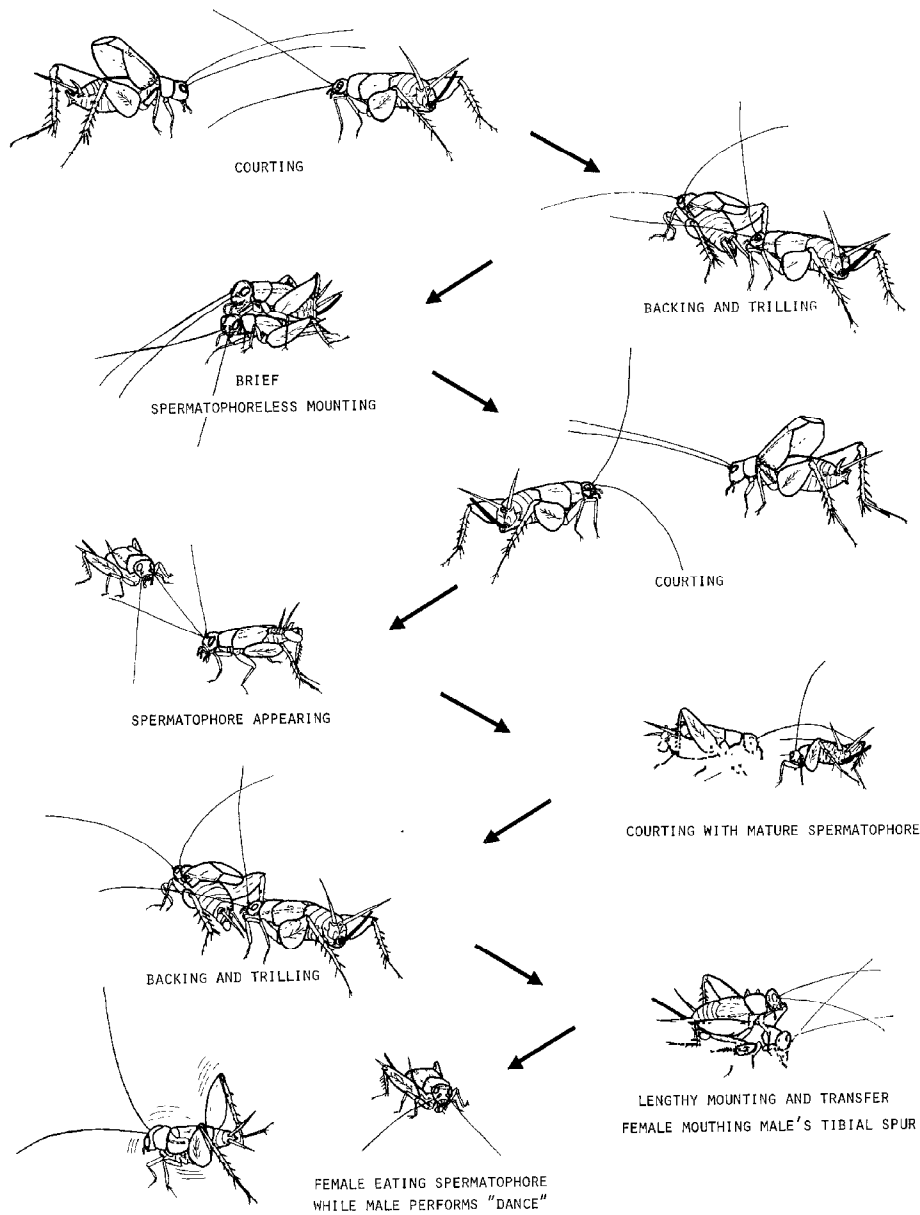


Fig. 3. Mating sequence in *Pteronemobius* subgenera *Allonemobius* and *Neonemobius*. Mating sequence in subgenus *Eunemobius* differs only slightly (see text) from the basic pattern shown here.

male to resume courting. If the female cannot be located, the male eventually removes the spermatophore with his hind tibia and eats it. After approximately 20 to 40 min of courting with the spermatophore (by this time it has darkened somewhat), the male turns around and trills continu-

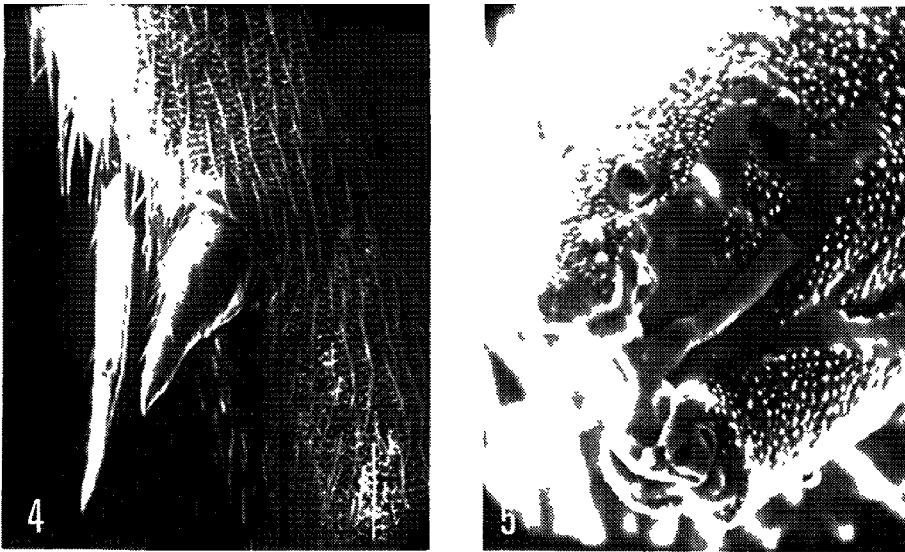


Fig. 4-5. Specialized tibial spur of *Pteronemobius* nr. *ambitosus* 531D. Fig. 4—Spur of virgin male with unmodified spur in background (200X). Fig. 5—Tip of spur which has apparently been opened by the female's mandibles during mating releasing the exudate (1200X). (Scanning electron micrographs made at Insect Attractants, Behavior and Basic Biology Research Laboratory, USDA, Gainesville, Fla. Courtesy P.S. Callahan, T. Carlisle and T. J. Walker).

ously, vibrating and swaying back and forth in front of the female much the same as before. The female mounts as the male pushes under and upward with his abdomen, finally engaging the female's genitalia. A pair usually remains coupled for 20 to 30 min. Shortly after coupling (0 to 5 min) the male brings 1 or both metathoracic legs forward and close beside his body. Now in an unnatural appearing posture, the internal proximal area of the tibia is in a position to be mouthed by the mounted female. Mr. Alberto Broce (1969 personal communication) examined the internal proximal tibial spurs of virgin and laboratory-mated males. In every instance where females mouthed the tibial region, the outer most portion of this spur was absent, whereas, the spines of unmated (virgin) males remained entire. Evidence of active chewing damage to a spur and the resulting exudation of a glandular substance, apparently fed upon by the female, is illustrated in Fig. 4-5. Field collected males of *P. ambitosus* (species complex) have more than 80% of their glandular tibial spurs damaged to this degree apparently as a direct result of females chewing and feeding on them during mating.

Mouthing of the spur area continues the entire time the female is mounted. She may mouth the pronotum-head area briefly in switching across to the opposite tibial spur, which may not have been brought forward yet. The pair disengages genitalia usually after the female walks off to one side. Occasionally the pair may remain motionless for a few min coupled in an end to end position prior to separation and female retention of the spermatophore. This end to end position appeared more often in the subgenus *Eunemobius* discussed below.

Upon separation, the male frequently jumps and jerks in sudden bursts. This "dance" was absent from the *sparsalsus* and *cubensis* mating sequences and in some of the mating sequences of the other *Pteronemobius* (*Allonemobius-Neonemobius*) species.

Following the dance, the male produces a long trill (similar to "courtship interruption"), a short series of chirps, or no sounds at all. Five to 10 min after uncoupling, the female removes the spermatophore by wiping it against the sand while backing up, and kicks at it with her hind legs. The female then searches the sand, recovers the spermatophore, and eats it. Some sort of male stridulation (calling, courting, or even "courtship interruption") is usually produced while the female eats the spermatophore. As soon as the female contacts the male (antennation) he begins to court. This marks the beginning of another mating sequence enacted exactly as before (including a spermatophoreless first mounting).

The Subgenus *Eunemobius*

The mating behavior of the 2 available species of *Eunemobius* (*melodius* and *carolinus*) is based on 2 complete and 2 incomplete sequences from each species. *Eunemobius* differed from the *Allonemobius-Neonemobius* studied in the following 7 ways. (1) The male stands in front of and faces away from the female during most all courtship phases. Antennation by the female apparently keeps the male stationary in 1 place. The male does occasionally antennate the female but usually during an initial encounter, when she is being pursued after leaving the male's vicinity, or occasionally when the male walks around the female during early stages of courtship. (2) Males appear to "dance" (jerking and swaying) in front of the female for a longer period prior to the first mounting. (3) During the first mounting, pairs coupled and jumped together violently at first, remaining mounted and connected considerably longer (20 sec for *carolinus* [n=1] and 14 sec for *melodius* [n=1]). The pair of *melodius* remained connected end to end for an additional 12 sec. (4) The spermatophore does not hang downward, but rather is tucked up against the venter of the male's abdomen during courtship. The abdomen is held low (<30°) with the legs extending nearly straight backward compared with the abdomen held high (>30°) and the legs bent at right angles in *Allonemobius* and *Neonemobius*. (5) The male stridulates almost continuously during courtship. (6) The male's metathoracic legs are held wide out to the side during the second mounting. (7) The second mounting (spermatophore transfer) in a single *P. melodius* mating involved 10 min of spur feeding followed by rotation to an end to end position held for 20 min; resumption of spur feeding for 25 more min followed rotation to end to end for at least 5 min prior to breaking genital contact. In a single *P. carolinus* mating the female began to rotate off the male after feeding on his spur for 33 sec, and eventually ended up making 3 1/4 complete 360° rotations to the left without ever uncoupling genitalia with the male! Both of these instances may represent atypical matings, yet are mentioned here because they contrast with the observations of *Allonemobius* and *Neonemobius*.

DISCUSSION

The significance of a *Pteronemobius* female mounting the male,

coupling briefly, and dismounting prerequisite to his producing a spermatophore is suggested through comparison with mating behavior in *Nemobius sylvestris* and *Hygronemobius alleni*. Nemobiine crickets that possess external glandular areas mouthed during mating (*N. sylvestris* and *Pteronemobius*) appear unique among gryllids in both the types of glandular structure and the length and complexity of the mating sequence. The mating system of these crickets appears derivative from the quick and simple mating systems represented by glandless *H. alleni* and presumably most other Nemobiinae.

Evolution toward fewer spermatophores with more safeguards that the female will be fully inseminated may explain the origin of glandular areas in *Nemobius* and *Pteronemobius*. The first mounting in *Pteronemobius* appears homologous to that in *Nemobius*, both being necessary for production of a large spermatophore. In *Nemobius* the spermatophore passed during the second mounting is 3 times the diameter and therefore 27 times the volume of the first. In *Pteronemobius* only the second mounting involves passage of a spermatophore. Female *Nemobius* do not always mouth the glandular areas at the base of the male's tegmina during each mount yet in *Pteronemobius* the glandular tibial spine is chewed upon extensively, but only during the second mount.

The extended coupling and spur feeding in *Pteronemobius* may function in allowing sufficient time for complete emptying of each spermatophore and keeping the female in the male's vicinity for another courtship sequence. Yet in *Oecanthus* (feeding on metanotal glands) and *Nemobius* (mouthing at the base of the right tegmen) females receive spermatophores during a brief coupling and then proceed to feed or mouth the glandular areas at length without the engagement of the genitalia. The 30 sec coupling *Acheta* and *Gryllus* was described by Alexander and Otte (1967) as necessary to complete the threading of the spermatophore into the female. This may instead be analogous to a post copulatory (i.e., post spermatophore tube insertion) act, holding the female as the spermatophore begins to empty. In *Oecanthus* and *Nemobius*, metanotal glands and glandular tegmina respectively serve this post copulatory function. *Pteronemobius* most certainly does not require 20 to 30 min to complete a threading process that is accomplished by *Nemobius* and *Hygronemobius* in a few seconds. Perhaps examination of the female spermatheca in both *Gryllus* and *Pteronemobius* will distinguish a copulatory act (coupling genitalia with spermatophore tube insertion) from a post copulatory-like adaptation (genitalia remaining engaged) that promotes full insemination. The 10 species of *Pteronemobius* studied here and *Nemobius sylvestris* show other similarities. Males of *Pteronemobius* subgenus *Eunemobius* court with their tails toward the female's head as in *N. sylvestris*. Actions of males searching for females that have left during a courtship sequence are amazingly similar. I believe Richards (1952) misinterpreted the actions of a *N. sylvestris* male when he wrote "... after mating [first mount] the male pursues the female as if to chase her away. . .", because similar actions were performed by *Pteronemobius* males following disturbances (by the observer) of the females they were courting. The males chirped loudly and followed the females around the cage apparently in an effort to re-establish contact. When contact was re-established the males resumed quiet courtship tones.

Comparing *Pteronemobius* with *Nemobius sylvestris* leads to a highly probable interpretation of the evolution of the first mounting (without a spermatophore) in *Pteronemobius*. In the *Pteronemobius* matings I have observed, spermatophore production was always preceded by the female mounting the male and their coupling genitalia briefly. The sequential nature of *Nemobius* mating (small spermatophore passed before the larger one is formed) suggests that the first may be of little or no value in inseminating the female and resembles a logical precursor of the *Pteronemobius* system. Using *Nemobius sylvestris* and *Hygronemobius alleni* to explain the origin of the spermatophoreless mount in *Pteronemobius* may be presumptuous in the absence of knowledge of mating in any other nemobiine genus. The possibility that a similar spermatophoreless mount occurs in *N. sylvestris* is supported by Richards' (1952) statement that the female ". . . makes several attempts to mount. . ." the male 30 to 45 min prior to passage of the first spermatophore. Could a brief spermatophoreless first mount have been overlooked in *N. sylvestris* as it apparently was for *Pteronemobius* by Fulton (1931) and Alexander and Otte (1967)?

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