The Mating of Tree Crickets

Their singing is a prelude to a fascinating array of reproductive strategies

by David H. Funk

At night, from late August until early October, old fields and woodlands across the U.S. reverberate with the melodious trill of crickets and katydids. To many human listeners the sound portends the passing of summer and the coming of fall; to others it provides a soothing reminder that the natural world is alive and well. To an entomologist the cacophonous singing of nocturnal insects is a signal that courtship, and with it the intense competition among males for females, is under way.

The most relentless and conspicuous of the nocturnal singers are members of the tree cricket subfamily Oecanthinae. Although they are in the same family (Gryllidae) as the more familiar black field crickets, tree crickets are smaller, ranging in size from 1.2 to 2.4 centimeters as adults, and they are pale green or yellowish in color. Moreover, as the name implies, they are mostly inhabitants of trees and tall shrubs, whereas field crickets are ground dwellers.

Of the 16 species in the U.S., the two that I have observed most closely are the broadwinged tree cricket *Oecanthus latipennis* and the two-spotted tree cricket *Neoxabea bipunctata;* both are common in the fields of southeastern Pennsylvania near where I live. Males and females of the two species mate repeatedly during the reproductive phase of their life, which generally lasts for from eight to 12 weeks, and an astute observer can readily spot courting males at night in the beam of a flashlight.

Males are easily recognized by the shape of their forewings, which are broader and more membranous than those of females. The overlying wing has an enlarged structural vein that acts as a file; when it moves across the underlying wing, which has a hardened margin that acts as a scraper, sound is produced [see "Cricket Auditory Communication," by Franz Huber and John Thorson; SCIENTIFIC AMERICAN, December, 1985]. Only males sing (as is the case for all crickets and most katydids), and their trill-like song, which is unique to each species, advertises a male's presence to sexually receptive females.

Receptive females approach males from the rear, because that is the direction in which most of the sound travels as it is amplified by and deflected off the wings. When a male senses the presence of an approaching female, he stops singing and turns around to touch her with his antennae. It is thought that by "tasting" her in this way he is able to confirm that she is a member of the same species and therefore an appropriate mate. The next stage in courtship involves an elaborate ritual (which varies slightly from species to species) during which the male again sings and exhibits other behavior such as rocking from side to side or pounding the substrate with his abdomen.

If the female is receptive to her suitor's overtures, she climbs onto his back and begins to feed on a special substance secreted from metathoracic glands near the top of his thorax, or wing-bearing section. The glands empty their secretions into a pit at the base of the male's hind wings, where they are readily accessible to the female once she is in the copulatory position. Although the secretions have not been chemically analyzed, they are highly attractive to females, and soon after a female begins to feed she will allow the male to mate with her.

Tree crickets package their sperm inside a hollow, nutrient-rich sphere called a spermatophore that is passed from the male to the female during copulation. Transfer takes only a few seconds, but for from five to 20 minutes afterward the female remains astride the male, feeding from his metathoracic secretions. As soon as she stops feeding and dismounts, the male resumes active courtship and will repeatedly attempt to back under her until she either remounts or wanders away. Such renewed activity on the part of the male may last an additional 20 minutes or more and is thought to be an important step in ensuring that large numbers of sperm pass from the spermatophore into a special sperm-storage organ in the female called the spermatheca. (When the female is ready to lay her eggs, sperm are released from the spermatheca and fertilize the eggs as they pass down the oviduct.)

The cricket spermatophore differs from the type found in most insects and other invertebrates in that much of it remains outside the female's

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MALE TREE CRICKET **Oecanthus latipennis** ***sings at night from August through October and in doing so advertises his presence to nearby females. Sound is produced when the forewings are rubbed together; the resulting trill-like song is species specific.***

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***TREE CRICKETS** are sexually dimorphic: males* (left) *have broad, membranous wings that they rub together to produce sound. Females* (right) *do not sing and have narrow wings that are held close to the abdomen.*

body after it has been transferred to her. Only a thin, threadlike tube enters the female; the ampulla, or main body of the spermatophore, dangles outside her genital opening. By curling her abdomen forward, a female can readily grasp the spermatophore with her mouthparts and remove it. Females always eat the spermatophore after copulation; they are thought to do so because the wall of the spermatophore contains nutrients that may enhance egg production. Males too will eat their own spermatophores (presumably for their nutritive value) if they are unable to transfer them to a female.

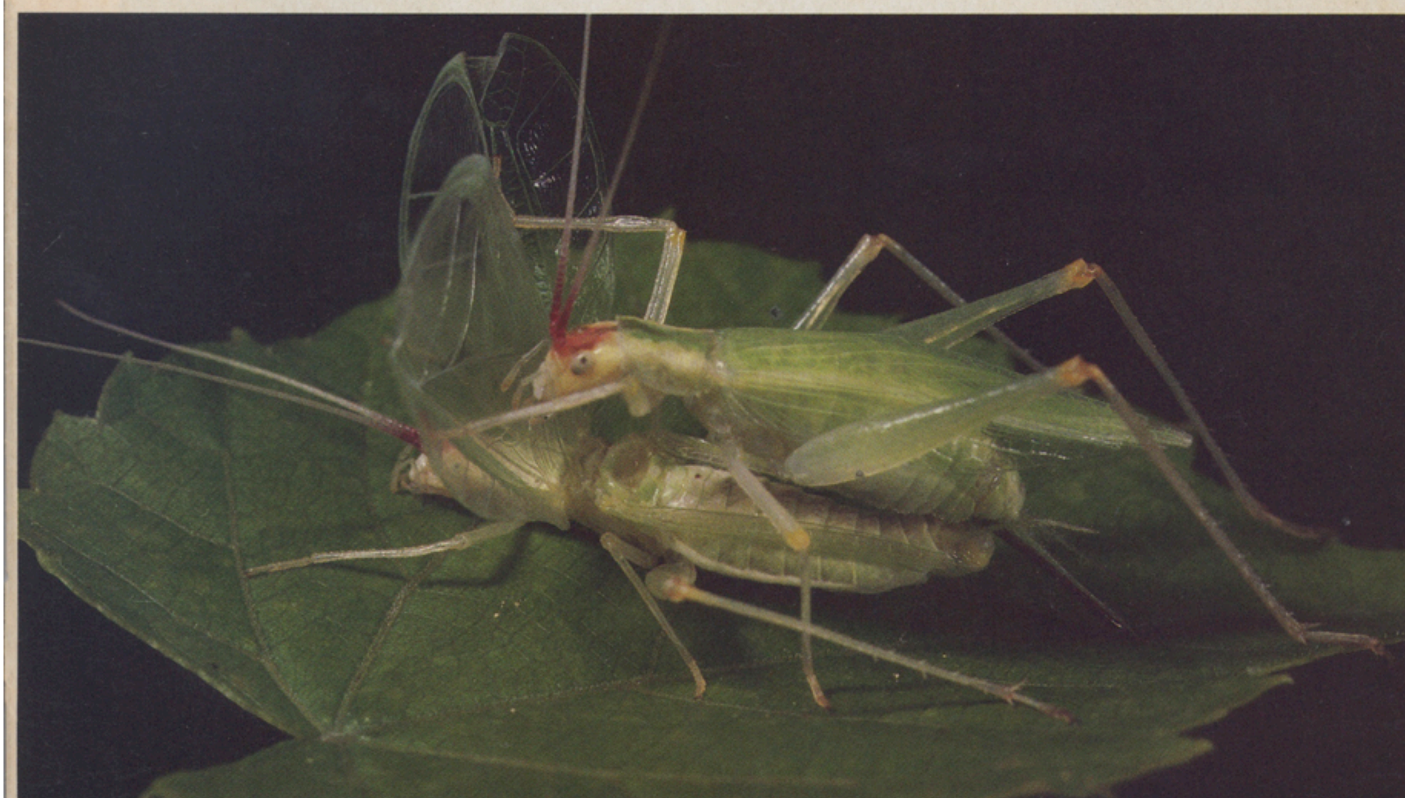
The glandular secretions and the external spermatophore of tree crickets make these animals interesting models for the study of sexual selection. First proposed by Charles Darwin in 1859 in his book *On the Origin of Species,* the theory of sexual selection (in contrast to the more general theory of natural selection) offers an explanation for why there are so many morphological and behavioral disparities between the sexes. As Darwin put it, sexual selection results from the constantly recurrent "struggle between the males for possession of the females." As a consequence of that struggle, natural selection has favored the evolution of traits, such as the antlers on deer or the red combs of roosters, that make a male physically competitive with other males or make

***AGGRESSIVE ENCOUNTERS** between males sometimes occur when two individuals are courting the same female. Their interaction is mostly a ritual in which both males wave their legs aggressively. Sometimes one male walks away, leaving the other to mate, but often the two fight until one literally kicks the other off the plant. (The female is not shown.)*

him more attractive to females—or that, in many instances, have both effects.

The concept of sexual selection has been expanded and refined since it was first proposed. It is now commonly believed that many behavioral differences between males and females are related to the size of their gametes and the degree to which each parent invests resources in his or her offspring. As a rule, sperm, which are small, are energetically relatively cheap to produce (they contain only genetic material), whereas eggs (which are larger than sperm and contain nutritive as well as genetic material) are not. The ability of a male to produce offspring is therefore limited largely by his ability to inseminate as many females as possible; in general males can maximize their reproductive potential by mating with multiple females, and to do so they often compete—sometimes fiercely—with one another. Females, on the other hand, produce relatively few eggs, and because each egg represents a substantial energy investment, a female can maximize her reproductive potential by mating selectively.

Consequently, in many insect (and other animal) species, after an elaborate courtship ritual the male will part company with the female almost immediately after he has inseminated her. Such a strategy is not universal, however, and it is less likely in species in which males provide females with a resource (generally a territory, a nest site or a food item) and thus contribute in a significant way—other than genetically—to the reproductive output of the female. In fact, many tree crickets, including *O. latipennis* and *N. bipunctata,* do not separate immediately after copulation but instead stay



DURING COPULATION the female sits astride the male and allows him to link his genitalia with hers. The actual transfer of the sperm-filled spermatophore, which is not visible, takes only a few seconds. The male's wings are held vertically during and after copulation; in that position his metathoracic pit is exposed and is accessible to the female.

AFTER TRANSFER of the spermatophore (the main body of which can be seen dangling from the tip of the female's abdomen), the couple disengage their genitalia. The female remains with the male, however, for 20 minutes or more, feeding on secretions that are produced by metathoracic glands located at the base of her partner's hind wings.

METATHORACIC-GLAND SECRETIONS are highly attractive to females. They collect in a special pit (left) *at the base of the male's hind wings, where they are accessible to the female when she is positioned above the male. Crickets (as well as other insects) package their sperm in a special sac called a spermatophore* (right), *which is transferred to the female during copulation. Only the threadlike portion, through which the sperm pass, is inserted into the female; the ampulla, or main body (which is about from one to four millimeters long depending on the species), remains outside her body.*

together while the female continues to feed from the male's metathoracic glands. Why should males, who might otherwise pursue additional females, continue to feed their mates after the transfer of the spermatophore?

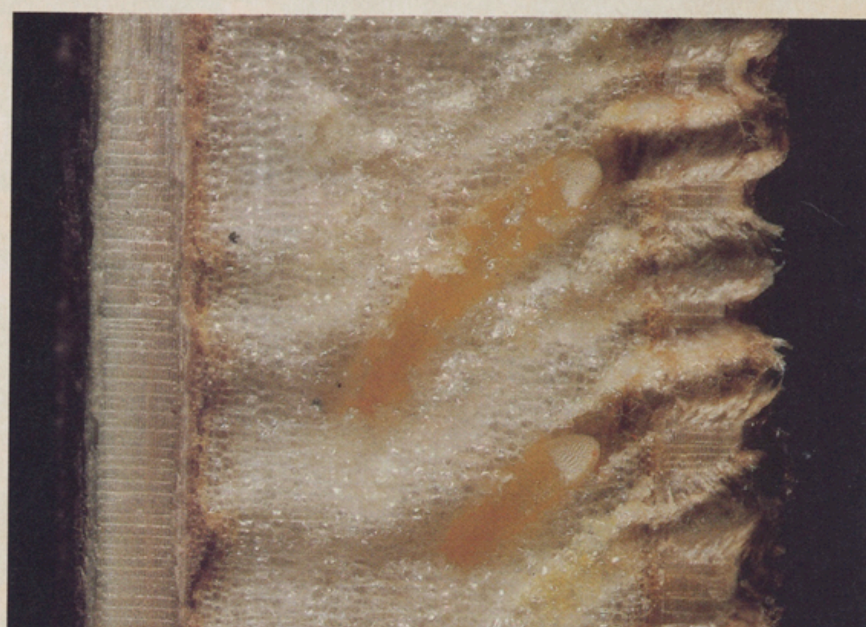
Although no studies have been done to show they contain valuable nutrients, the male's metathoracic secretions may contribute in some nutritive way to egg production. By providing his mate with nutrients that enable her to produce more eggs or larger ones, a male can effectively increase his own reproductive output. Even if the secretions do not enhance egg production, it is clear they serve another important function: they distract the female so she will not remove the spermatophore until it has been emptied.

If the female removes the spermatophore before all of the sperm pass out of it, the male has wasted part of his reproductive potential. In some cases a female who has mated previously, and therefore already has a sufficient supply of sperm in her spermatheca, may mate with a male simply to obtain the nutritive rewards of his spermatophore. The fact that many females tend to remove the spermatophore before it has been emptied of sperm supports that hypothesis.

From the male's point of view, of course, mating without insemination represents lost time and energy (in the form of spermatophores, glandular secretions and, in some species, body parts), and selection therefore strongly favors males who have strategies for ensuring successful insemination.

Males of *N. bipunctata*, for example, have evolved a secondary strategy for minimizing the premature departure of the female and thus maximizing their reproductive potential. In addition to secretions, they have evolved a behavior that prevents the female from leaving before most of the sperm have passed from the spermatophore into the spermatheca.

Males hang upside down from the leaves or twigs of trees when they are courting and will allow a female to mount them only while they are in that position. Once the female has mounted, the male drops his hind legs, maintaining his hold on the tree with his first two pairs of legs. That frees the hind legs for the next step: as soon as the spermatophore is transferred to the female, the male begins to shake rapidly while moving his hind legs back and forth along the body of the female. This behavior may persist for as long as 45 minutes, during which time the female is more or



FEMALES DEPOSIT their eggs in plant stems (top). *The needlelike ovipositor (seen protruding from the abdomen) is inserted at almost a right angle into the stem's pithy interior. (The two appendages near the tip of the abdomen are cerci; they are sensory in function and occur in both sexes.) Females of some species lay their eggs in rows: the ovipositor is inserted, an egg is laid and the ovipositor is withdrawn and then reinserted a millimeter or so down the stem. Four holes and two eggs are visible* (bottom) *in a longitudinal section of a stem enlarged 20 diameters.*

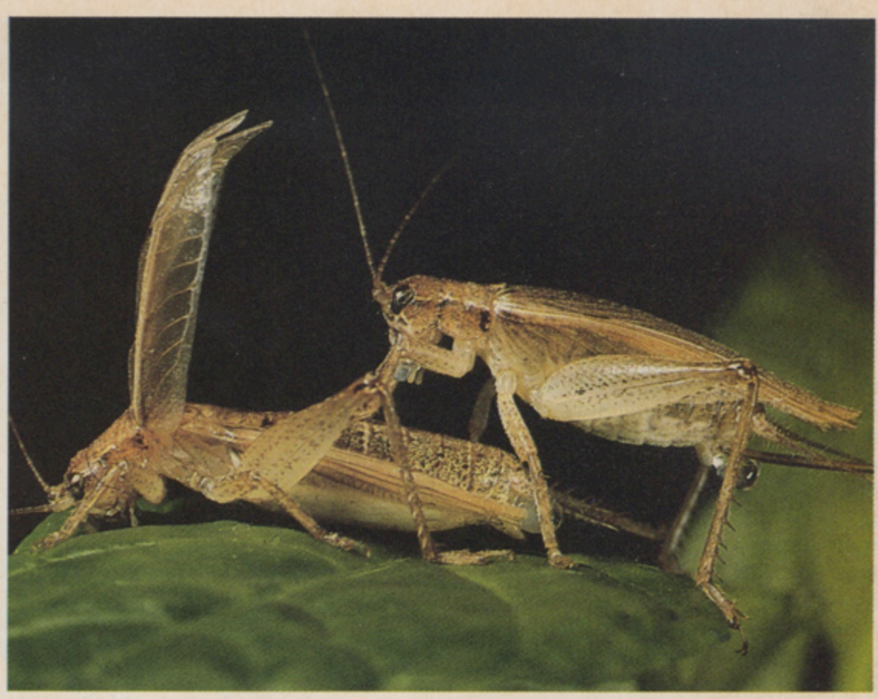
TWO-SPOTTED TREE CRICKET Neoxabea bipunctata *has an unusual mating strategy: couples hang upside down, and the male moves his hind legs back and forth along the body of the female. The movement of the legs is thought to prevent the female from leaving the male before most of his sperm have passed from the spermatophore into her body.*

AFTER THE FEMALE leaves the male, she curls her abdomen forward and removes the spermatophore with her mouth. She then eats it. The spermatophore, which is now emptied of most of its contents, is thought to be a source of nutrients.

less trapped by the living fence her mate has created around her. Mating pairs of two-spotted crickets are highly conspicuous during this phase and can be easily located with a flashlight even when they are high in a tree. Eventually the male stops moving, and the female dismounts, whereupon she removes the spermatophore and eats it.

Other cricket species have evolved different strategies for preventing females from leaving before the spermatophore is empty. Richard D. Alexander of the University of Michigan and Daniel Otte of the Academy of Natural Sciences of Philadelphia have found, for example, that males of the restless bush cricket *Hapithus agitator* (subfamily Eneopterinae) retain the attention of a female by letting her nibble at their forewings for 10 minutes or so during copulation.

Males of another eneopterine cricket, *Orocharis saltator*, produce a long series of spermatophores—as many as 20—during a single sexual encounter. The spermatophores differ from those of many crickets in that each contains relatively few sperm (about a tenth as many as are in a typical *Hapithus* spermatophore).



SPERM TRANSFER in the bush cricket,* Orocharis saltator, *resembles an assembly line. The first spermatophore was removed by the female soon after she received it and is now being eaten by her. After she removed the first spermatophore, the male produced a second one, which he has transferred to the female, who is still eating the first one. Meanwhile the male has produced a third spermatophore, which he will give to the female as soon as she removes (and begins to eat) the second one.

Sperm transfer in *Orocharis* takes place in assembly-line fashion: immediately after receiving her first spermatophore, the female will back away from her partner and in doing so will drag her abdomen across a leaf, dislodging the spermatophore, which she then begins to eat. A minute or two later the male, who has produced a second spermatophore, will attempt a second mating. If the female is receptive to his overtures, she climbs onto his back where she continues to eat the first spermatophore while being inseminated with a second. When she has finished eating, she again dismounts, removing the second spermatophore, which she also eats. Meanwhile the male, who has produced a third spermatophore, initiates yet another coupling. The entire sequence is repeated many times: I have seen mating pairs remain together for as long as three and a half hours, during which time the male produces a continuous flow of spermatophores. Because it takes about nine minutes for a female to consume one spermatophore but only about four minutes for sperm to empty from the spermatophore, it appears that sequential spermatophore production in *Orocharis* serves to distract the female in much the same way that metathoracic secretions do in *Oecanthus*.

Sexual selection is clearly responsible for the diverse array of mating strategies seen in crickets. Beyond that, many questions remain. Perhaps the most interesting is the extent to which males contribute nutritionally to egg production. Resources such as secretions and spermatophores help to ensure insemination, but do they also lead to the production of more or healthier offspring?

Studies by Darryl T. Gwynne of the University of Toronto indicate that in some katydid species the male produces an enormous spermatophore representing as much as 40 percent of his body weight. The spermatophore is far larger than is needed for insemination: a large portion of it consists of a nutritive covering that contributes to egg production. In other species, however, the spermatophore has only a small nutritive covering. Scott K. Sakaluk of Illinois State University has found, for example, that in one species of cricket the spermatophore covering is only large enough to distract the female during insemination.

One possible explanation for this disparity is that the size of a male's contribution reflects the number of partners a female is likely to have during her reproductive life. If the number is high, as it is in many crickets, one male's nutritional resources may end up supporting a competitor's offspring. Therefore, in species where multiple matings are common, selection should favor males who provide resources that are no larger than are necessary to ensure insemination. Although such modest contributions are unlikely to satisfy a female's nutritional demands, males are unlikely to compromise their ability to secure additional mates by investing in offspring of dubious paternity.

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