Reproductive Behavior (T. G. Forrest)

Male calling

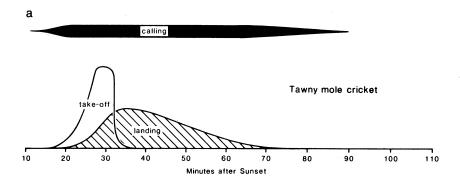
Adult male mole crickets, like most other crickets, produce a calling song that functions to bring the sexes together. Females sometimes respond to the call by walking or flying to the male (phonotaxis) and mating with him. Songs of crickets inhabiting the same area at the same time are usually species-typical—that is, each species has its own calling song and a trained ear can easily tell the species of cricket by hearing its song. Tawny and southern mole cricket calling songs are continuous trills that differ in both the tone (carrier frequency; 3.3 vs. 2.7 kHz respectively) and pulse rate (wingstroke rate; 130 vs. 50 pulses per sec) of the song. Songs of tawny mole crickets are characteristically "buzzy" and have short intermittent silent periods of less than 1 second. Southern mole cricket songs are more musical and continuous. Both songs can be heard soon after sunset coming from the ground where males call from specially excavated chambers.

The calling chamber opens at the soil surface through a trumpetlike (exponentially expanding) horn. This chamber is constructed each evening 10 to 20 minutes before calling and is tuned by the cricket to the frequency of his calling song. The tuning increases the efficiency of sound production by at least threefold. Intensities of calling songs range from 50 to 90 dB (relative to $20\mu N/m^2$) at 15 cm and are dependent upon male size and soil moisture.

The calling period is correlated with female activity and flight periods. Male tawny mole crickets begin calling 10 to 20 minutes after sunset, and southern mole cricket males start 15 minutes later. Calling continues for about one hour (Fig. 12).

Flight

About the same time in the evening that males are building their calling chambers, many females and some males are preparing for flight. A small opening is made at the soil surface where the individual returns periodically, seemingly to check weather conditions.



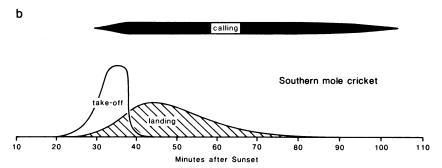


Fig. 12. Timing of flight and calling for (a) tawny and (b) southern mole crickets. Dark bars indicate when males of each species call. Unshaded curves show the distribution of take-off times; shaded curves show the distribution of landing times. Both species fly and call for little more than an hour beginning shortly after sunset, with tawny mole crickets preceding southern mole crickets by 5 to 15 minutes.

Just prior to flight, while remaining inside its tunnel, the cricket warms its flight muscles by trembling. When the muscles are warmed and all is clear, the cricket runs from the burrow and immediately takes to the air. Crickets usually remain in flight 5 to 20 minutes, but some may fly more than 40 minutes, perhaps traveling as far as 8 km (5 miles). Flight usually ends in response to the male calling song (Fig. 12); however, crickets are also attracted to and land near lights.

Phonotaxis and mate choice

Mole crickets calling near one another must compete acoustically for flying females, and females hear many calling males during a single flight. If differences in calling songs are cues to differences among males that are related to increases in female reproduction, females should respond to and mate with some males more than others. In general, females respond only to calling songs of their own species, but within each species some males' songs are more attractive than others. A single male may attract as many as 27 females in one calling period, while other males calling nearby attract few or none. One aspect of the calling song that enables females to discriminate is intensity. Flying mole crickets prefer to land at louder calls. Louder males attract more females (and males, see below) than less intense males, and the effect is greater than would be expected just because a louder call travels farther.

Two factors that influence the loudness of a male's call are his size and the moisture content of the soil used to construct his calling chamber. Other things being equal, a large male produces a louder calling song and attracts more females than smaller males. Thus by going to louder calls, females choose to mate with larger males. However, only about 30% of attracted females enter the burrow of the calling male whose song triggered their landing. The others land nearby and dig their own burrows, probably using the loudness of the call to locate moist soil for oviposition. After the calling period is over, males (those that have called and those that have landed near the caller) probably search for, court, and mate with these females (Fig. 13).

Males also fly and respond to calling songs in much the same manner as females; that is, they preferentially land at louder calling songs. They thereby find an area where many females may have landed. Such males sometimes enter the caller's burrow and fight with him. Males may also use the louder calls to detect areas with high soil moisture that will make their own calls louder and enhance their ability to attract females.

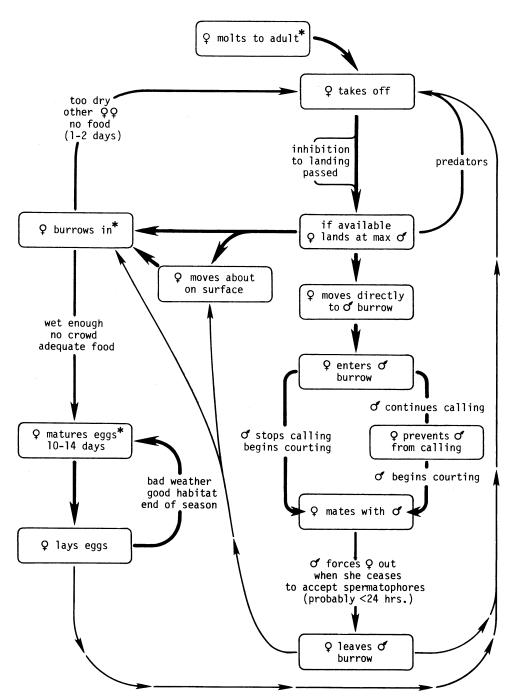


Fig. 13. Female reproductive behaviors. Behaviors indicated by heavier arrows are better documented than those indicated by lighter arrows. (*Females may mate with males that find them in their burrows.)

Mating behavior

Since most of the sexual behavior of mole crickets is subterranean, few observations of their mating behavior have been made. Whether or not males and females find each other by means other than phonotaxis is not known, but courtship songs are heard at all times of the day, indicating that phonotaxis does not always immediately precede courtship and mating.

When males and females meet in a burrow, they often antennate each other. Males may produce several sharp "aggressive" chirps followed by softer courtship chirps. If the female is unreceptive, the two will fight. During these bouts males and females produce aggressive chirps, and bite and claw each other with forelegs until one is driven from the burrow. If, on the other hand, the female is receptive, the male will continue courting her acoustically, his forewings slightly raised, producing rhythmic chirps often followed by short trilling sequences. The courtship songs have similar tones and pulse rates to the calling songs. The rate of the chirps varies in the courting sequence and may depend on the female's behavior. Male tawny mole crickets often hit their pronotum against the roof of the burrow producing a rapid thumping sound (15 to 20 hits per second, 5 to 10 hits per burst, repeated at 1 to 2 second intervals). Pronotal thumping may convey special information to the female or other nearby crickets. It has not been observed in southern mole cricket males or in females of either species.

If the male is facing the female in the burrow, he backs up while continuing his courtship song. The female follows. The male, still courting, turns to face away from the female. The male sometimes pushes soil ahead of him in the burrow, enlarging the tunnel to make room for the female to mount. As the female approaches, the male lowers his wings and tries to back under her.

Coupling does not occur until about 40 seconds after mounting. At this time a small spermatophore is extruded from the end of the male's abdomen. The pair couple briefly, the spermatophore is passed to the female, and she dismounts. The spermatophore is white and ovate, about 1 mm in diameter, with a short curved tube on one side. The tube is inserted into the female, and the sperm empties from the spermatophore through the tube into her spermatheca, or sperm storage organ. The small spermatophore is completely concealed under the female's subgenital plate to protect it from being dislodged by the tunnel walls.

Once the female dismounts, the male remains stationary for 8 to 10 minutes and then resumes courting. Sometimes he stops to enlarge the tunnel. This stationary period is needed for the male to form a

new spermatophore. During the male's inactivity the female moves about the tunnel, feeds, or grooms. When the male begins the next courtship sequence, the female removes the spermatophore and may eat it. The female may mount and copulate with the same male several times, but once the female becomes unresponsive to the male's courtship attempts, they fight until one of the pair leaves the burrow system. During her adult life a female usually mates with more than one male.

Egg laying and hatching

A male's parental duties are over after mating, but the female must find suitable oviposition sites. Mole cricket dispersal flights are adaptive in that already mated females can leave unsuitable areas (for example, areas with poor food, high density of crickets, or low soil moisture), locate, land, and oviposit in newly opened habitats. These flights have contributed to the mole crickets' range expansion and increasing pest status in the southeastern United States.

By landing near calling males, females can locate suitable mole cricket habitats. Flying females are generally in an early stage of a reproductive (clutch) cycle. Their primary oocytes are small, suggesting that an egg clutch was laid just prior to flight. After landing, the female spends 9 to 14 days maturing oocytes and then lays a clutch of eggs (Fig. 13).

About 40 (25 to 60 depending on female size and age) gray or brownish eggs are laid in a small ovoid (4×3 cm) chamber or egg cell. Egg cells are constructed by females less than 24 hours before oviposition at depths of 9 to 30 cm, depending on soil type and moisture. Once oviposition is complete, the female seals the entrance to the chamber with soil and has no more contact with eggs or young. Females sometimes lay more than one clutch before they fly again and may mate with another male between egg clutches.

During the 20 days it takes the eggs to develop, they double in volume from water absorption, and their color changes from gray to milky white. All eggs of a clutch usually hatch within a 24-hour period. Hatchlings are white or yellowish and turn bluish-black within 24 to 48 hours. Juveniles often eat the egg shells (chorion) and are known to cannibalize siblings. They escape from the egg cell through a small tunnel dug straight up to the soil surface.