SUB-SOCIAL BEHAVIOR IN A BURROWING CRICKET *ANUROGRYLLUS MUTICUS* (DE GEER)

ORTHOPTERA: GRYLLIDAE

MARY JANE WEST AND RICHARD D. ALEXANDER

Museum of Zoology and Department of Zoology, The University of Michigan, Ann Arbor

Sub-social behavior, or specialized parent-offspring interaction that terminates before the offspring mature, has been noticed in a wide variety of arthropods: millipedes, centipedes, scorpions, pseudo-scorpions, crustaceans, spiders, mites, web-spinners, cockroaches, earwigs, treehoppers, shield-backed bugs, giant water bugs, beetles, wasps, and bees. Except for wasps and bees, it has been described in detail in only a very few cases, perhaps most notably the earwig, *Forficula auricularia* L. (Fulton, 1924; Weyrauch, 1929). This is surprising in view of the extent of investigations on the truly social insects (ants, wasps, bees, and termites) and of efforts to reconstruct the sequences of change by which they have evolved their distinctive characteristics: division of labor, sterile castes, and complex communication (Wheeler, 1923; Michener, 1953, 1958; Evans, 1958).

Various authors have mentioned that some female mole crickets (Gryllotalpinae) isolate themselves in their burrows with the eggs, live beyond the hatching of the eggs, and display hyper-aggressiveness in this situation (Hayslip, 1943; Hahn, 1958). Females of *Brachytrupes achatinus* Stoll (Brachytrupinae), the "big brown cricket" of India, deposit their eggs shallowly in the end of one of their galleries and the young nymphs leave the parental burrow a few days after hatching (Ghosh, 1912). Liebermann (1955) noted that the female short-tailed cricket, *Anurogryllus muticus* (De Geer) (Brachytrupinae), lives in the brood chamber until the second or third molt of her offspring. This paper reports some details of parent-offspring interactions in the short-tailed cricket, discusses their adaptive significance, and hypothesizes that certain morphological and behavioral characteristics of non-social and sub-social crickets pre-adapt for the evolution of greater complexity in parent-offspring interactions.

We have raised five families of *Anurogryllus* to partial maturity in the laboratory, and in one case were able to watch and photograph during a period of several weeks the behavior of a female in a burrow which she had excavated in sand along the glass wall of a jar (fig. 1–6). This female was collected as a juvenile in Kannopolis, North Carolina, on May 25, 1961; she mated in early June when a male was first placed in her cage. Single matings per female are not otherwise known in crickets, but after mating once, this female showed only aggressive behavior toward males that were placed in her cage and then watched continually while they courted her for long periods, both inside and outside burrows. During the weeks following her mating, the female excavated an underground chamber into which she carried particles of apple, peach, and grass supplied in the cage, and from which she ousted intruding males and females alike. In expelling one male which we had purposely introduced into her burrow she actually tore off one of his hind legs (fig. 2); after repairing the damage to the burrow entrance, she ate the severed leg (fig. 3). Although we have watched several thousand cricket fights involving approximately 30 species in four subfamilies and ten genera, this is our only record of definite physical damage; and it is apparently the only clear record of cannibalism as a result of cricket aggression. Both facts are surprising, for the males of this species are the most successfully territorial and the least violent of burrowing crickets in their aggression (Alexander, 1961); additionally, in this case the male did not at all reciprocate the female's aggression. Aside from this species, intense aggression among crickets is known to occur only in males, and only when both individuals are hyper-aggressive.

On July 16, the female was found to have in her chamber a pile of 16 eggs and 4 first-stage nymphs. During the next two weeks she remained in the burrow, concentrated most of her actions in the burrow chamber, and repeatedly carried out several specific actions in connection with eggs, nymphs, food, fecal pellets, substrate particles, and external disturbances. These several actions were alternated with each other, and with long periods of immobility spent without exception near the eggs, short exploratory trips around the burrow, and grooming of various portions of the body.

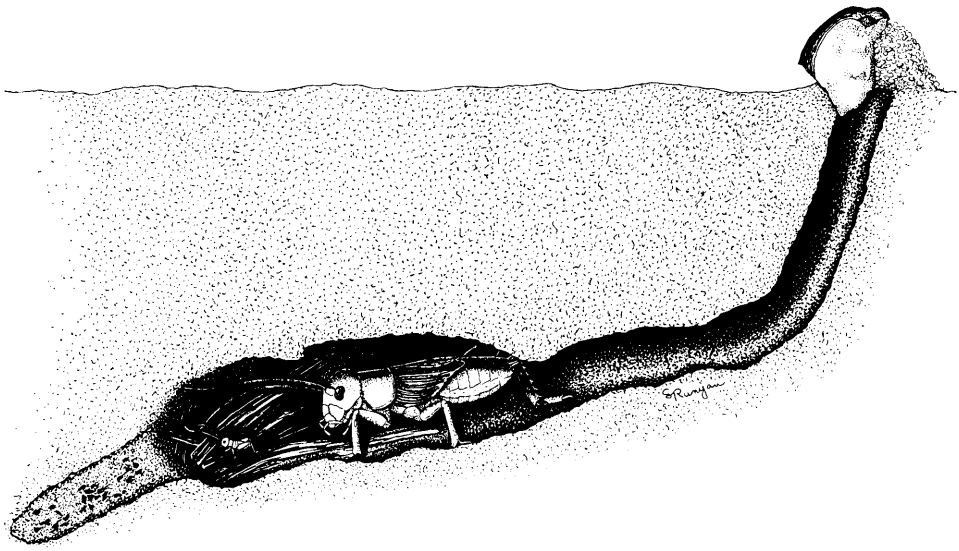

FIGURE 1. Female of *Anurogryllus muticus* (De Geer) in brood chamber with new pile of cut grass stems. Note antennal contact between juvenile and female. Filled defecation chamber is at left. Egg pile is partly covered with sand near female's left front leg. Tunnels leading into the interior of the jar in which the female is confined begin directly on her right. The female burrowed up under chunks of apple as shown and plastered substrate particles being removed from the burrow alongside the apple, creating "push-ups" of the sort indicated. The female's hind leg was lost while she was a juvenile. All illustrations for this paper were drawn from photographs made through a glass side of this female's burrow. Prints from all photographs used will be filed with a reprint of the paper in the Orthoptera library of the Insect Division, University of Michigan Museum of Zoology.

Two kinds of eggs were deposited: normal-sized, all of which eventually hatched, and miniature (unfertilized?), all of which were eventually seized, carried off, and eaten by the juveniles. During egg-laying, the female turned so that the tip of her abdomen was near the egg pile; immediately afterward the female always turned about, picked up the new egg, and placed it on the pile. Previously laid eggs were frequently palpated, mouthed (picked up, turned about in the mouthparts, briefly inserted partway into the mouth, and dropped again or pushed away with one foreleg), piled and repiled, and sometimes covered with food or substrate and later uncovered. Miniature eggs seized by the nymphs were sometimes retrieved temporarily by the female, which chased the nymph, seized the egg directly out of the nymph's mouthparts, and replaced it on the pile. Certain eggs received all or nearly all of the female's attention for extensive periods, and one egg-sized pebble was mouthed and kept on the pile for a time. The eggs of this cricket are shorter and more bluntly rounded at their tips than those of related field crickets which inject their eggs into the soil (fig. 5).

If the burrow entrance was opened or disturbed, the female immediately ran

to it, shook her body in the manner characteristic of aggression in many kinds of crickets, and began to close it again by removing pieces of substrate from the tunnel wall and plastering them near the entrance with her head and forelegs. Other disturbances, such as jarring of the cage or increases in light intensity, always caused a reaction—either a slight rearing-up indicative of aggressive response in a cricket (Alexander, 1961) and slight movement toward the disturbance (fig. 5), or else a change from immobility to exploratory movement or manipulating of the eggs. If disturbed slightly when not directly over the eggs, the female immediately moved to them, often beginning to palpate or mouth the eggs and move the pile. Only the most violent substrate vibration caused her to retreat into the interior portions of the burrow.

The female showed little reaction to the young nymphs, which were gregarious and remained near the female, usually clustered on the roof of the chamber touching her antennae or moving about her body and under it (fig. 1). When she moved, the nymphs followed. Two portions of her body seemed especially attractive: the mouthparts and the tip of her abdomen. Nymphs sometimes stood with their mouthparts in contact with the female's mouthparts for several seconds, and one nymph stood for about a minute on its hind legs, propped against the female's hind leg, with its antennae apparently against the female's miniature external ovipositor. When a nymph touched the female or walked across her body, she either gave no reaction or moved only slightly; once she pushed a nymph off her back with a grooming movement of the hind leg. When she contacted a nymph with her mouthparts, she either palpated it or actually picked it up and very briefly manipulated it in her mouthparts in a manner resembling the mouthing of eggs. When a similar-sized *Gryllus* nymph was forced into her burrow, she similarly picked it up briefly and dropped it unhurt from the mouthparts, then showed no further reaction. On the five occasions that a miniature "trophic" egg was laid while we were watching, it was seized by one or more nymphs and either eaten on the spot or carried off. The nymphs quickly gathered around these eggs and violently competed for their possession. This competition for individual food particles, as well as transport of food particles, and burrow excavation similar to that of the adults by removal and transport of individual substrate particles, are actions that in very young juveniles are unique to *Anurogryllus*; they appear in the other crickets that we have studied only during the late juvenile and adult stages. The only reaction of nymphs to normal eggs was an occasional examination with the mouthparts, especially with the palpi. Grass, rotten peach, and apple were also eaten by the nymphs, but without the avidity with which they consumed the miniature eggs. The small number of normal eggs laid by this female (20 to 25 compared to 100 to 300 in other crickets) may be related to her single mating; both characteristics, as well as the trophic eggs, are probably advantageous because of their association with transfer of the female's energy into a prolonged behavioral maximizing of the chances of success of individual hatchlings, through both feeding and protection.

Defecating behavior was remarkably consistent in the female. She backed into the lower corner of her chamber, deposited a pellet, and resumed her position near the eggs. Five or ten minutes later she returned to the spot, picked up the fecal pellet, and carried it out of the chamber through one of the two exit tunnels. This happened six times during our observations. The defecation corner was originally a short, downward-sloping tunnel. Later it was filled with a dark, streaked material, apparently defecatory products (fig. 1), suggesting that fecal pellets deposited before the tunnel was filled were not removed. After the tunnel was filled, one or more pieces of substrate were often removed after removal of the fecal pellet itself. No other materials were ever carried out of the chamber, and only food was carried into it.

This female displayed the usual reactions of *Anurogryllus* males, females, and juveniles to different food materials (Alexander, 1961). She burrowed up under

pieces of apple and peach (fig. 1), and removed and transported bits of them into the chamber. She pulled and cut into short lengths long stems of grass inserted into her burrow (fig. 4). All of these materials were then piled, usually on top of the eggs, but occasionally beside them (fig. 1). Within 24 hours she had always piled food and eggs separately. Occasionally, the female alternated in succession the acts of placing an egg to one side and a bit of food to the other.

The female died August 1. Her offspring remained in the chamber until she was dead, and the corpse and the juveniles both disappeared into the inner portions of the burrow during the first night. The corpse was probably dragged away by other crickets with burrows in the cage, but under usual circumstances there is little doubt that the female's own offspring would consume it, the female thus providing food for her offspring not only by what she had accumulated in the burrow prior to death, but also by the presence of her own body decaying there.

Some of the actions described above are known in remarkably parallel form in other sub-social insects. Interaction with eggs, for example, is almost identical in earwigs and crickets; Weyrauch (1929) found that a female earwig accepted proper-sized paraffin eggs but rejected pricked, rough eggs, and that eggs deprived of parental care became moldy and discolored and did not hatch. Many arthropods show specialized defecatory behavior, for example, the moth ear mite, *Myrmonyssus phalaenodectes* Treat, in which the actions are very similar to those in *Anurogryllus* (Treat, 1958). Trophic eggs are well-known in ants; some queens feed them to their first offspring, and first instar larvae are sometimes fed exclusively on worker-laid eggs (Brian, 1953; E. O. Wilson, personal communication). But trophic eggs have not been previously described in a sub-social insect.

As suggested by Alexander (1961), many characteristics of burrowing crickets seem pre-adaptive for the development of social interactions. Thus, crevice-inhabitation and territoriality, exhibited to one degree or another by nearly all surface-dwelling crickets, concentrate activity in specific locations; without this prerequisite, burrow elaboration, which may require days of excavation in one location, could not proceed. Elaboration of the burrow and of burrowing actions in turn require increasing manipulative ability and increasingly refined sensory discrimination, especially with regard to size, shape, and nature of substrate materials. The manipulative actions that a female cricket uses in handling her eggs, food, nymphs, and fecal pellets all appear to be identical to elements of burrowing actions existing in related, non-social crickets which do not transport food or fecal pellets; and they may all have been derived from burrowing actions. If so, the burrow not only provides a suitable location for eventual ensconcement with eggs and juveniles and their protection from some kinds of potential predators, but its evolutionary elaboration also incidentally develops capabilities prerequisite for sub-social interactions. In addition, cutting, transport, and piling of various food materials is accomplished by manipulative movements which appear to derive from burrowing actions, and discrimination among different substrates, reflected

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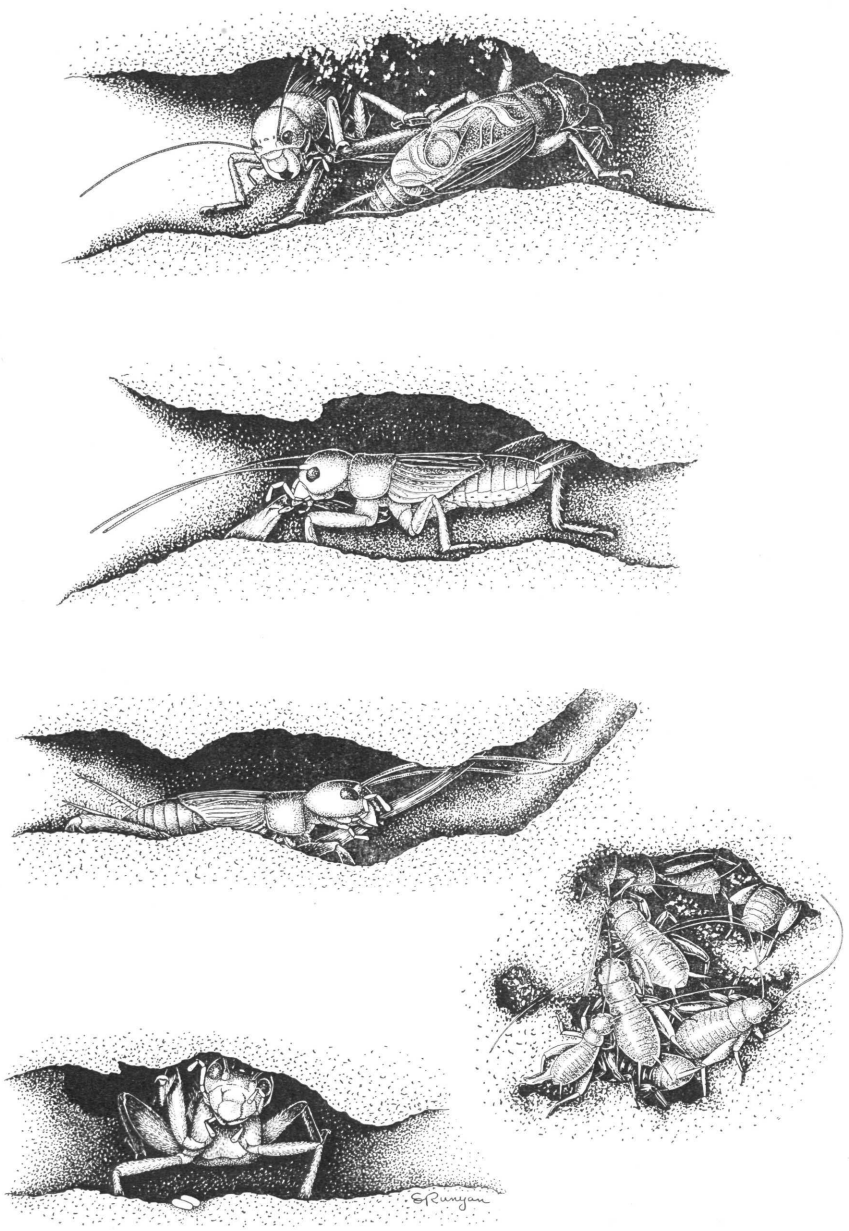
EXPLANATION OF FIGURES II–VI

FIGURES 2–6 (top to bottom). FIGURE 2. Female ousting an intruding male from her burrow by kicking him after tearing off his right hind leg with her mandibles. Note the male's lop-sided position, and the retracted labrum and spread mandibles of the female. FIGURE 3. Female eating the male's leg after tearing it off while ousting him. She has closed up the hole by which he left the burrow. FIGURE 4. Female cutting grass stem with her mandibles after pulling it into her burrow. Note position of the antennae. FIGURE 5. Female responding to bright light by rearing up, approaching the glass side of the brood chamber, pressing against it, and touching it with her forelegs and maxillary palpi. Temperature change may be involved. Note egg pile between her front legs. FIGURE 6. Juvenile crickets (probably second and third instars) disturbed by breaking burrow above them. This is about the age at which the female dies and the juveniles begin to fend for themselves. These juveniles are more plump and soft-bodied than those of most other crickets. This picture is more highly magnified than figures 2–5. Drawings were prepared by Miss Suzanne Runyan, museum artist.



Figures 2 to 6

in different kinds of burrowing actions (Alexander, 1961), may be related to eventual discrimination between substrate and food. In this connection, deep-burrowing, sub-social crickets (Gryllotalpinae, Brachytrupinae) apparently differ from all other crickets in that they require moist food for survival, and cannot exist on dry food and a separate water supply. This feeding restriction may be related to the fact that sub-social females do not eat the eggs during incubation, for non-social crickets are essentially omnivorous and characteristically dig up and eat their own eggs with great relish if exposed for long periods to the oviposition site.

Finally, the hyper-aggressiveness which in non-social, burrowing crickets is associated with the burrow only in the male, and is functional chiefly in insuring that he can retain his stationary and secure signalling location, must have evolutionary significance with regard to the hyper-aggressiveness and invincibility of the sub-social female in the burrow with her eggs and offspring.

All of the characteristics described above as pre-adaptive for social existence in crickets appear first in surface-dwelling, non-social crickets (*Nemobius, Acheta, Gryllodes*) and are increasingly evident as one compares genera that are increasingly subterranean (*Miogryllus, Gryllus, Scapsipedus*) and approach in one way or another the elaborate expression of sub-social behavior described here for *Anurogryllus* (Alexander, 1961).

SUMMARY

Females of the short-tailed cricket, *Anurogryllus muticus* (De Geer), ensconce themselves in burrows after mating and remain there until death, which usually occurs when the juveniles have reached about the third instar. Approximately 25 normal eggs are deposited in an enlarged chamber, and the female repeatedly "mouths" them and keeps them piled together. One female observed for several weeks ousted an intruding male, piled various kinds of food separately from the eggs, defecated in a special lower tunnel, and eventually began to lay miniature eggs. The juveniles competed violently for these eggs and eventually ate all of them. It is suggested that the small eggs were unfertilized, and that they represent a specialization similar to the so-called "trophic" eggs of ants. Various feeding, burrowing, and aggressive actions of surface and subterranean crickets are interpreted as pre-adaptive for the appearance of sub-social behavior.

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