Botany-Zoology 106

Experiment 7: BEHAVIOR ASSOCIATED WITH REPRODUCTION IN FIELD CRICKETS

Introduction

Behavior has been described as "what an animal does." Some activities are easily labelled behavioral, such as running, walking, swimming, sleeping, eating, drinking, fighting, courting, mating, burrowing, and so forth. Others might be less positively called behavior, such as release of adrenalin into the blood, change of color (such as blushing), or certain activities of the central nervous system (such as worrying or remembering).

As with morphology and physiology, behavior is part of the animal phenotype, and, therefore, always a product of hereditary and environmental influences. While it is obviously impossible, and not particularly important, to label precisely all characteristics of the phenotype as being behavior, morphology, or physiology, nevertheless, some useful comparisons can be made. For example, behavior is generally more directly subject to natural selection than morphology or physiology. Behavior has even been defined, somewhat jocosely, as "what animals have interposed between natural selection and the morphological and physiological aspects of their phenotypes." Behavior is also more indirectly related to the genotype. In other words, behavior is usually the end-product of exceedingly long chains of physiological events, and, partly as a result, variations in behavior that have nothing to do with hereditary variations are frequently much more prominent than similarly non-hereditary morphological and physiological variations. In terms of our ability to observe and measure, behavior is probably the most diverse aspect of the phenotype. Behavioral differences are often abundant between species, or even individuals, that cannot yet be distinguished morphologically or physiologically.

We usually think of anatomy and physiology as being somehow more basic than behavior -- of behavior as being something that simply derives automatically from underlying morphological and physiological characteristics. In one sense this is certainly true. Sometimes, though this line of thinking leads to the assumption that one cannot really study behavior fruitfully until he knows all (or at least a great deal) about anatomy, physiology, and development -- or even that one only needs to study anatomy, physiology, and development. When we consider the direct relationship between behavioral variations and selection, however, it becomes clear that, in the evolutionary sense, behavior is actually responsible for the nature of the anatomy and physiology that underlies it. In other words, if a particular behavior pattern, say, pattern X, is what is really important to the animal's survival, then selection will automatically favor any anatomical-physiological background that will most consistently and surely produce behavior X (and concomitantly cause the least harm -- or the most good -- to the rest of the animal's performance in life). There might be a dozen different changes that will, for example, cause an animal to run faster, leap higher, or find food or mates more quickly. In this sense, anatomy and physiology exist to serve behavior.

These are a few of the reasons why we cannot hope to understand animals very well unless we know what they do, or how they behave, and what their behavior does for them, or how it functions. In this exercise you will first see various aspects of cricket behavior and carry out some manipulations that will cuase changes in the behavior, then infer from your observations and experiments how these aspects of cricket behavior may promote the survival and reproduction of the individuals possessing them.

Cricket Behavior

Under natural conditions male field crickets call (chirp or trill), principally at night, when they are ready to copulate. Sexually responsive females find males by moving toward their calls, and each species that breeds in a certain area at a

certain time has a distinctive calling song (fig. 7). The sound-producing organs are on the front wings, the auditory organs on the forelegs (figs. 1-3). Males have prominent veins in their forewings that females lack, and females have a long ovipositor or egg-layer protruding from the tip of the abdomen. Juveniles lack wings or have only tiny wing pads (fig. 2).

Most males live in burrows, under stones or logs, or in soil crevices. When populations are dense, many individuals can be found crowded together; when they are sparse, calling males are rarely closer together than a few feet. In the latter case, a male may live in the same burrow or crevice for days or weeks. He usually dashes straight into his hole if disturbed. Adult crickets usually live 6-8 weeks.

Experimental studies have indicated that certain events may change a male's aggressiveness, or his ability to win fights. You will carry out a series of observations and manipulations to see whether (1) living in isolation, (2) mating, (3) inhabiting a burrow or niche, and (4) losing or winning fights influence a male's aggressiveness. At the end of this laboratory period you should be able to write a short essay explaining how acoustical signals, aggressiveness, burrowing, and the behavior that immediately follows copulation ordinarily function in the lives of field crickets. You should be able to explain how the responses you observe combine to maximize a given male's chances of having his genes extensively represented in the next generation.

Materials for Each Group of 2-4 Students

1. Two terraria about two feet long and eight inches wide
2. Four pint or quart jars with ventilated tops
3. Three cardboard cylinders about 3/4 inch in diameter and 1½ inches long ("burrows")
4. Paint ("airplane dope") and a camel's hair brush for marking crickets
5. Four pieces of glass suitable for partitioning the terraria into three chambers each
6. Six adult male field crickets, three adult females, two juveniles (use eight males, four females, two juveniles, if they are available). Half of all males will have been kept crowded together in a terrarium for several days prior to the laboratory period, the rest in isolation in the screen-top jars. The females and juveniles can be kept together. None of the adults will have mated, and all will be at least seven days adult.
7. A camel's-hair brush for nudging or guiding crickets
8. A few large vials into which crickets can be guided for transfer from one cage to another

Note: During the following observations, take special precautions to avoid disturbing the crickets by your presence. Do not touch the table on which the terrarium rests except when changing the setup. Crickets are extremely sensitive to substrate vibrations, and one of their responses to disturbance is to stop moving for periods from a few seconds up to a minute or so. Do not move quickly near the terrarium or "tower" over it, as they are also sensitive to changes in light intensity. They are likely to perform better if there are no bright lights nearby. To secure maximal activity, subject the crickets, during the week preceding the laboratory, to 12 hour periods of dark and light alternated, so timed that the dark period ordinarily begins approximately when the laboratory begins.

If your crickets accidentally seem to miss ever coming into contact, you can sometimes assist in a profitable way by gently urging or herding them in the desired direction with a camel's hair brush. Such interference should be kept to a minimum, and cannot be used when certain kinds of comparisons are to be made.

Procedure

1. Place in one terrarium (fig. 4) three (or four, depending on the number of males available) males taken from the group that has been kept crowded together. Mark the males, or otherwise distinguish them, and give each a name, number, or other special designation.

Watch this group of crickets for about ten minutes, noticing all encounters. Try to distinguish different kinds of encounters, for example, "no-aggression" encounters and aggressive encounters. Further, distinguish, if you can, mildly aggressive and violently aggressive encounters, and see if you can tell who "wins" or "dominates" aggressive encounters. Refer to these three kinds of encounters as types (1), (2), and (3). If one cricket dominates, indicate this in your notes by writing that cricket's name (or designation) as the numerator, and the defeated individual's name as the denominator. Thus, A/B (3) could mean that cricket A defeated cricket B in a violently aggressive encounter.

Your objective in this exercise is to compare aggressiveness under different conditions. You now have several means of comparison. First, for the whole group of crickets you can compare (1) total number of encounters in a timed period, and (2) average intensity of aggression. For any individual you can compare (before and after giving him some particular experience) (1) whether he defeats some other particular cricket, and (2) how hard he fights when he encounters some other particular cricket.

Having settled on the method of watching and recording observations, now watch for a timed period of 30 minutes, recording the number of encounters and the nature and outcome of every encounter. Optimally, you should see all of the different possible pairs of crickets meet, most of them more than once.

Is there a dominance hierarchy or "peck order"? That is, can you predict outcomes of encounters on the basis of how previous encounters come out? Is there a male who defeats all other, another who defeats all but the dominant individual, and so forth? Do not be annoyed or disturbed if most of these crickets seem entirely passive and non-aggressive. Remember that your observations will be valuable only if they are carefully and objectively recorded so that you can make comparisons.

2. Now separate the three males you have just watched by partitioning their terrarium so that each male is penned alone. Put two juveniles in with the dominant male and watch their behavior for 15 minutes. Are they aggressive? What do they do when the dominant male behaves aggressively toward them?

Now provide each of the subordinate males with a cardboard tube partly buried in the sand at an angle so that only its opening protrudes. Leave them alone now, but keep a watch on their behavior.

3. Place together in the other terrarium a group of three males that were previously in isolation and watch them for 30 minutes, keeping the same kind of record as for the previous group. Does their behavior differ from that of the males that formerly had been crowded together? Are they more aggressive or less? Can you tell what actually happens during a fight? Can you tell what causes the fight to stop? What do you think a male does that enables him to win?

4. Now pen off the two subordinate males in the second hierarchy you have (presumably) established and provide each male with two females. Watch for 10 minutes, or until one or more of them has copulated. Do males and females fight one another? Can you tell what stops the male from fighting? Compare this with the male's behavior toward juveniles. Notice that, in the presence of females, the male produces a sound different from the fighting chirps, and he holds his wings differently to make it. This is called the "courtship song." The third principal signal of field crickets is the calling song, already mentioned in the introduction; it may be produced during this exercise by some of your males when they are alone, especially in burrows (fig. 6).

Can you tell what happens during mating? Do you see a white object pass from the male to the female during mating and remain attached to the female after mating? This is a spermatophore or sack of sperm (fig. 5). Pluck it from the female immediately following mating and crush it on a slide, cover with a cover slip, adding some saline solution, and examine it under a microscope. If you do this carefully, you should see living sperm. In crickets, insemination occurs after mating has terminated. The spermatophore empties in about 15 minutes. In view of this fact, consider the significance of the male-female interaction following copulation. What ultimately happens to the empty spermatophore?

Crickets are not the only insects in which the female climbs on the male's back during copulation; they share this behavior with cockroaches, various katydids, mayflies, scorpion flies, and others. Neither are they the only animals that inseminate by means of a spermatophore; so do most insects, scorpions, Peripatus, millipedes, salamanders, sharks, and many bony fish. Most or all animals evidently mated this way during the time in their history that they were first emerging to land life.

5. Allow an unmated male to enter the compartment with a male that is subordinate to him, but has just mated. Who dominates? Was the fight more or less intense than those occurring when this particular pair met before?

6. Remove the female soon after a pair has mated. What does the male do? Place the female back in the cage. What does he do now? If possible, exchange females between two males after two pairs have mated. What happens?

7. If one or both of the males in the other terrarium with a cardboard "burrow" has been acting as though he's "at home" in it, cause a male previously dominant to him but currently not owning a burrow to enter his chamber and touch antennae with him. Compare the intensity of the fight and its outcome with their previous meetings. What happened? Now bring together the burrows of two males, both of which are acting as though they're at home in the burrow, and place the entrances together, facing one another at an angle. Cause a female to walk between them, or entice the males together by gently tickling one with a hair or a camel's hair brush. Try to make your tickler as much like the touch of a cricket's antenna as possible. If the cricket dashes away or leaps, you're too crude. What happens? How intense is the aggression?

8. If you have remaining time, mix up the crickets as you wish and try to predict hierarchies or winners of particular encounters. Watch until the end of the period. All of the things you have seen, or were asked to watch for, can be observed in a single compartment with males, females, juveniles, and burrows all together. It sometimes takes longer, but often more of interest happens in this kind of situation than in the more contrived circumstances.