

SOUND PRODUCTION AND ASSOCIATED BEHAVIOR IN INSECTS¹

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The number and variety of insects which produce sounds with specialized apparatus undoubtedly exceed those of all other living organisms combined, but only a few of these, the crickets, katydids, grasshoppers, and cicadas, make noises loud enough to be noticeable to man. These are the so-called singing insects, and their ancestors may well have been the first organisms on earth to communicate through sound waves transmitted in air.

Although often obscured today by the intense and endless noises of civilization, insect sounds must have been among the loudest and most persistent sounds heard by primitive man. Their effect is apparent in art, mythology, and literature, and it may be more than mere coincidence that the chant, often called the most ancient of human music, bears a striking resemblance to the tuneless and repetitious insect song.

Scientific interest in insect sounds dates at least to Aristotle, who over two thousand years ago separated two groups of Homoptera on the basis of whether or not they could produce sounds (Myers, 1929, p. 81). Today a complete bibliography on sound production and perception in insects would contain several thousand references.

Until recently, studies of insect sounds had to be based on human auditory impressions. For this reason, the variety and complexity of structure in insect sounds, chiefly involving pulsations delivered too rapidly for the human ear to perceive, are only beginning to be realized. Magnetic tape recorders and electronic sound analyzing devices now provide objective means of analyzing and comparing these intricacies of structure, and have been responsible for a surge of interest in insect sounds in many different parts of the world (Busnel, 1954; Pringle, 1956).

Potential applications of studies of insect sounds are many and varied. Insect sounds have long been used in systematics (Fulton, 1931, 1932, 1952; Davis, 1928; Pringle, 1955), and in studies of ecological and geographical distribution (Faber, 1929, 1932); they show promise of being valuable in control (Robertson, 1944; Kahn *et al.*, 1947; Kahn and Offenhauser, 1949; Vanderplank, 1948; Busnel, 1956), and in fundamental studies of behavior and physiology (Pringle, 1954, 1956).

Sound production and perception have arisen in the insects a large number of times, and consequently a wide variety of structures is involved (Kevan, 1954). Sounds are produced by insects in five different ways: (1) by rubbing one body part against another, *i.e.*, stridulation (crickets, katydids, grasshoppers, bugs, beetles, moths, butterflies, ants, caterpillars, beetle larvae, others); (2) by striking some body part, such as the feet (band-winged grasshoppers), the tip of the abdomen (cockroaches), or the head (death-watch beetle) against the substrate; (3) by vibrating some body part, such as the wings, in air (mosquitoes, flies, wasps, bees, others); (4) by vibrating drum-like membranes called tymbals (cicadas,

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leafhoppers, treehoppers, spittlebugs); and (5) by forcibly ejecting air or fluid (short-horned grasshoppers).

The auditory organs of insects generally involve tympanal organs or hair sensilla. They differ from those of mammals and birds in being relatively insensitive to fluctuations in frequency, but are apparently capable of responding to high-speed intensity modulations (Pumphrey, 1940). It is in this character of rhythm and speed of pulsations that a wide variety of patterns exists, both in the sounds of different species of insects, and in the different sounds of a single species. The ability of an insect to discriminate between the various rhythms of its own species, or to single out the sounds of its own species from those of others is largely untested, and represents one of the most fascinating aspects of the study of insect acoustics.

Sound-producing and auditory structures may involve almost any part of the insect's exoskeleton. In different groups, such organs have been found on the mandibles (Acrididae), palpi (Tridactyloidea), antennae (Phasmidae), head capsule (Anobiidae), pronotum (Cerambycidae), mesonotum (Elateridae), metanotum (Prophalangopsidae), forelegs (Tettigonioidea), middle legs (Lucanidae), hind legs (Passalidae), forewings (Tettigonioidea, Acridioidea), hind wings (Acridioidea), several of the abdominal segments (Coleoptera, Orthoptera, Homoptera), and the cerci (Blattidae). Many species possess two sets of sound-producing organs (Corixidae) or auditory organs (Gryllidae).

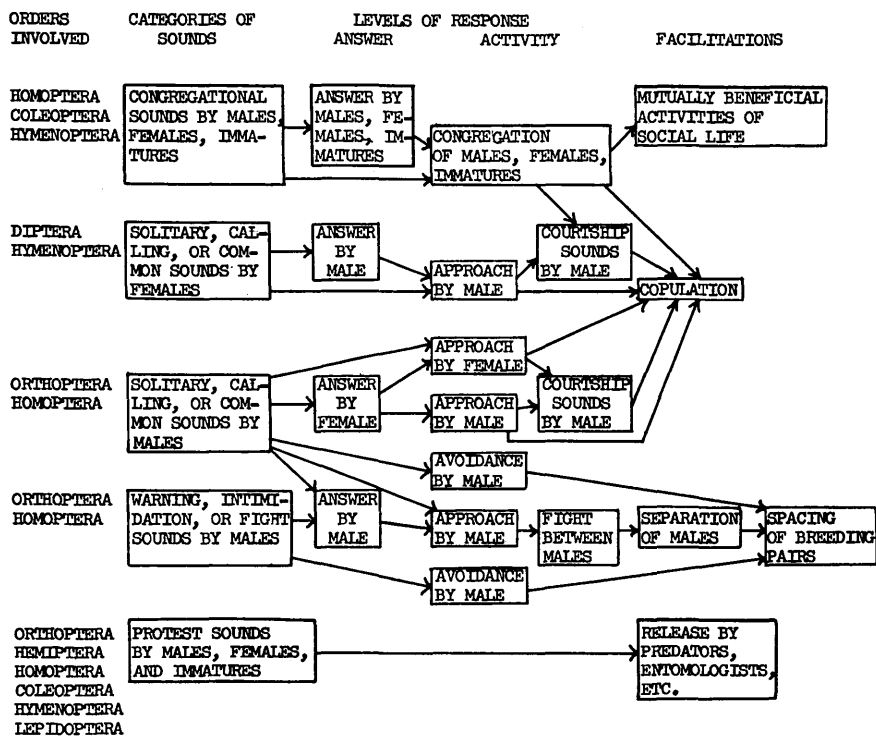
Insects produce sounds in two general types of situations. First, there is a group which includes the crickets, katydids, grasshoppers, cicadas, leafhoppers, and possibly many others, the adult males of which produce sounds more or less continuously throughout daily periods which are apparently determined by light intensity and possibly by temperature or humidity or both. The sounds produced by some of these insects are the loudest and best-known of insect sounds, and are those that we have come to call "songs," probably because they generally consist of rhythmical repetitions of the same phrases. Since these songs are the insect sounds which are most often heard, they have received such labels as "common" songs and "ordinary" songs. They have also been called "solitary" songs since in the singing Orthoptera they are often inhibited by the presence of other organisms (situations involving other organisms evoke sound responses of different nature). They function in bringing the adult males and females into close proximity (at least in some species), either by (1) causing the female to move to the male (crickets), (2) causing the female to make a sound which attracts the male and enables him to locate her (slant-faced grasshoppers), or (3) causing congregation of large numbers of males and females (cicadas). Knowledge of these functions has caused such names as "calling" songs and "congregational" songs to be applied to these sounds.

The second general type of stimulus situation includes those situations in which the sound is elicited directly as a result of the presence or activities of other organisms. The sounds produced in such situations can be divided into four categories: (1) those produced by males, females, or immatures as a result of the presence or activities of animals of other species—disturbing, capturing, or holding them—and referred to by such terms as "alarm" cries, "distress" calls, "protest" sounds, or "congregational" sounds; (2) those produced by a male in the presence of a female of the same species, generally called "courtship" or "mating" songs; (3) those produced by a male in the presence of another male of the same species, generally called "warning," "intimidation," or "fight" sounds; and (4) those produced by a female in the presence of a male of the same species.

The types of behavioral sequences that have been observed in connection with sound production in insects are summarized in textfigure 1. Sounds placed in the same categories because they are produced in similar situations often occur

in several different orders. These are not homologous, however, and in many cases sounds in the same category have arisen independently a number of times within a single order or family. Specialized sound production that probably has a common origin in two or more families is known in only two orders, the Orthoptera and the Homoptera.

To illustrate some of these different kinds of sounds and the situations in which they are produced, representatives of three orders are discussed below.



TEXT FIGURE 1. Behavioral sequences associated with insect sounds.

All sounds were recorded at a tape speed of 15 inches per second, the cricket and beetle sounds with a Magnecorder, Model PT6A, the cicada sounds with a Magnemite, Model 610EV. An American Microphone Company D33A microphone was used for all recordings. The audio-spectrographs, or Vibragrams (Plates I to IV) were made with a Vibralyzer, the use of which is explained by Borror and Reese (1953). In all Vibragrams displayed here, frequency is portrayed on the vertical axis, time on the horizontal axis, and relative intensities by the darkness of the mark. The sound pulses portrayed in figure 1 are of a relatively pure frequency, making at this particular setting of the Vibralyzer approximately the same type of mark as would electronically produced pure frequency signals. The wide range of frequencies which appears in figures 4 to 6 is also present in the sound portrayed in figure 1 but is masked by the dominant pure frequency. As this dominant pure frequency disappears from the sound (transition to courtship), a stepping-up of the gain to produce a comparably dark picture brings out the soft frequencies.

*Acheta assimilis Fabricius*²
(Orthoptera: Gryllidae: Mountain Field Cricket)

The sounds of field crickets are produced by vibration of the tegmina, or forewings. As the tegmina are closed, a transverse row of minute teeth (file) on the lower side of the upper tegmen near its base is scraped by a dorsally-projecting sharp-edged structure (scraper) on the median edge of the lower tegmen. In the calling song the tegmina are held at a 45° angle with the body; in courtship they are lowered and tilted roof-like over the abdomen. In the calling song of the mountain field cricket (fig. 1), the tegmina are vibrated at a rate varying from 15 strokes per second at 50° F to 29 strokes per second at 100° F. A concomitant change in the dominant frequency occurs, indicating that this pure frequency is a function of the speed of wing motion, and probably corresponds to the number of file teeth struck per second, as suggested by Lutz and Hicks (1930).

If a culture of field crickets containing several adult males and females is kept under observation, it is soon noted that some sort of sound is being produced by one or more of the males almost continually. A few distinct types of sounds gradually become apparent to the observer, as do the situations in which they are produced. Eventually one becomes able to describe relative positions of different individuals in the culture and the types of activity in which they are engaged without looking at them solely by the types of sounds being produced by the males.

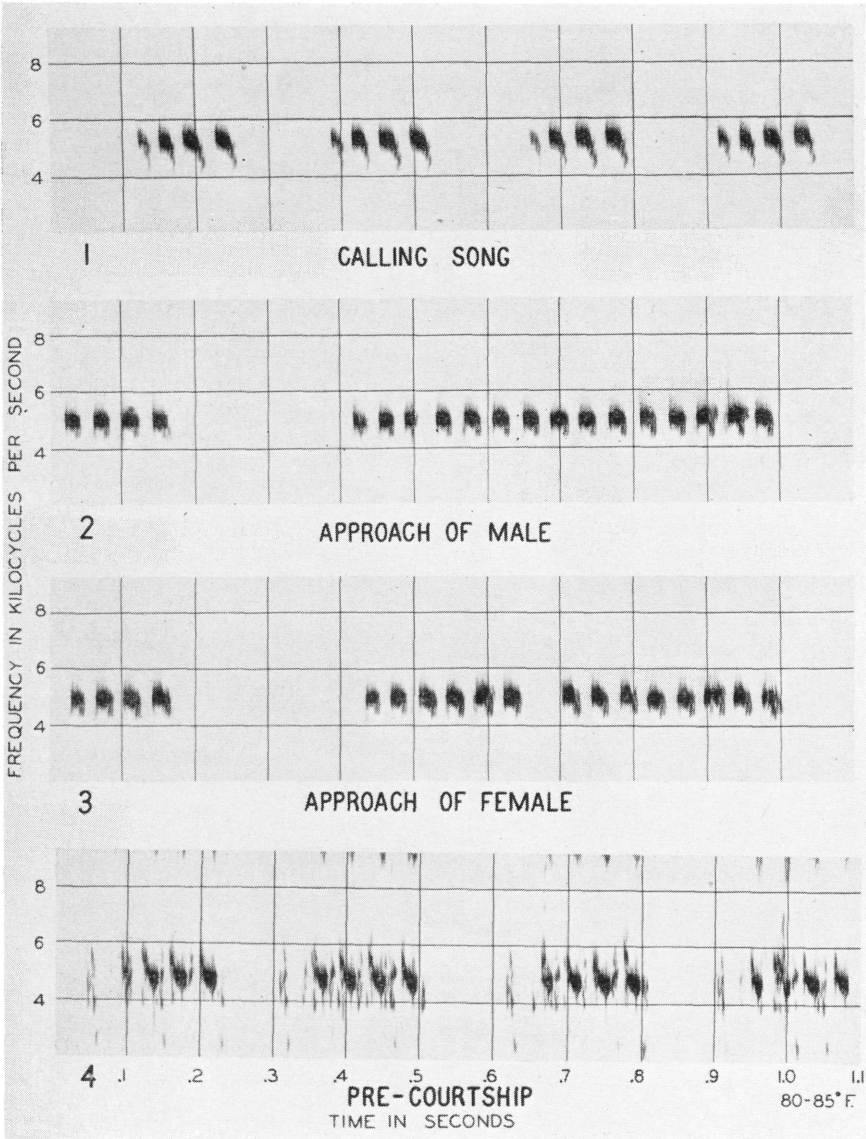
As with most singing Tettigoniidae and Gryllidae, male field crickets tend to space themselves in the field, and to remain in one spot all their adult lives. A large part of the time, both day and night, they produce the calling or solitary song (fig. 1). This song attracts the females, which move toward and locate the males.

When a singing male is approached by another male, he stops the regular chirping of the calling song and delivers one or more louder, clearer, and longer chirps³ (fig. 2). The two individuals may stand an inch or so apart, facing each other, and chirp in this manner for several seconds, or they may move together and engage the mandibles and scuffle, sometimes turning and kicking each other with the hind legs. Eventually one male leaves, sometimes after only exchanging chirps, sometimes after physical contact in which he may lose a leg or have his tegmina torn.

When a male singing the calling song is approached by a female, or sometimes when a male walking around his "territory" encounters a female, he will usually produce a few chirps very similar to those produced when another male is encountered *i.e.*, loud, clear chirps containing a large number of pulses (fig. 3). The chief difference between this type of chirping and that produced in an encounter between males is that it grades continuously into what has been arbitrarily designated as "pre-courtship singing" (fig. 4) and, if uninterrupted, eventually into "mixed courtship singing" (fig. 5), and "full courtship singing" (fig. 6). Pre-courtship singing is made up of softer, less musical chirps than those produced in the calling song, and mixed courtship singing consists of a mixture of the soft pulses produced in full courtship with louder, clearer pulses resembling those of the calling song. Full courtship singing consists of a rhythmical repetition of

²The several species of native *Acheta* (field crickets) in North America have thus far been designated by colloquial names only. The individuals discussed here were from the spring brood of the mountain cricket of Fulton (1952), and were collected in Franklin County, Ohio.

³The term "chirp" is an English word of common usage denoting any short, sharp animal sound, and has been generally used by entomologists to refer to intermittent types of stridulation as contrasted with more or less continuous trilling. In the present paper the term "pulse" will be used to refer to the sound made by a single movement of the sound-producing apparatus, and "chirp" will refer to short groups of pulses (fig. 1 portrays four 4-pulse chirps).



many-pulse chirps, each of which terminates in a louder, clearer "tick," represented in figure 6 by the slender vertical mark between pulse groups.

Mixed courtship singing is the type of courtship most commonly heard in a culture. It apparently represents a stage between pre-courtship and full courtship which is maintained for long periods of time when the female is not fully stimulated by the courtship activities of the male. This may be due to her physiological condition, or to some weakness in the courtship sequence, as often occurs when a male of one species courts a female of another species. As long as the female remains in the vicinity of the male but does not allow him to back under her or come into physical contact, the mixed courtship song is the type produced.

If a female leaves a courting male, or another male approaches while a male is courting, he delivers the loud, clear, many-pulse type of chirp (fig. 7, 8) which is also characteristic of the male and female encounters. Sometimes, after producing the full courtship song for a minute or so without success (with the female standing immobile, or at least not moving away), a male will deliver a few of these louder, sharper chirps; turn around and face the female; caress her with his antennae; and begin the mixed courtship singing, slowly turning around and backing toward the female again. If a female withdraws upon being contacted by a courting male, he may deliver a few sharp chirps and then perform the same sequence of activities, or he may merely shift his singing somewhat toward the calling song (that is, by injecting more of the clear, musical pulses which appear now and then in mixed courtship singing) and continue to back toward her.

During courtship singing, in addition to backing toward the female, the male sways from side to side and flattens his body against the substrate, especially as he comes into contact with the female. If the female is responsive, she either mounts on top of the male's flattened tegmina, or allows him to back under her, and the spermatophore is transferred in this position. The courtship song either may be necessary for successful copulation, or it may shorten the time between the meeting of the sexes and copulation. It is possible that the motion of the tegmina is more important than the sound produced during courtship. Most of the crickets which do not possess courtship songs have dorsal female-attracting glands which draw the female into the copulatory position. In the tree crickets (Oecanthinae), this gland is located on the metanotum while in the ground crickets (*Nemobius* spp.), it has developed in connection with a spine at the base of the hind tibia.

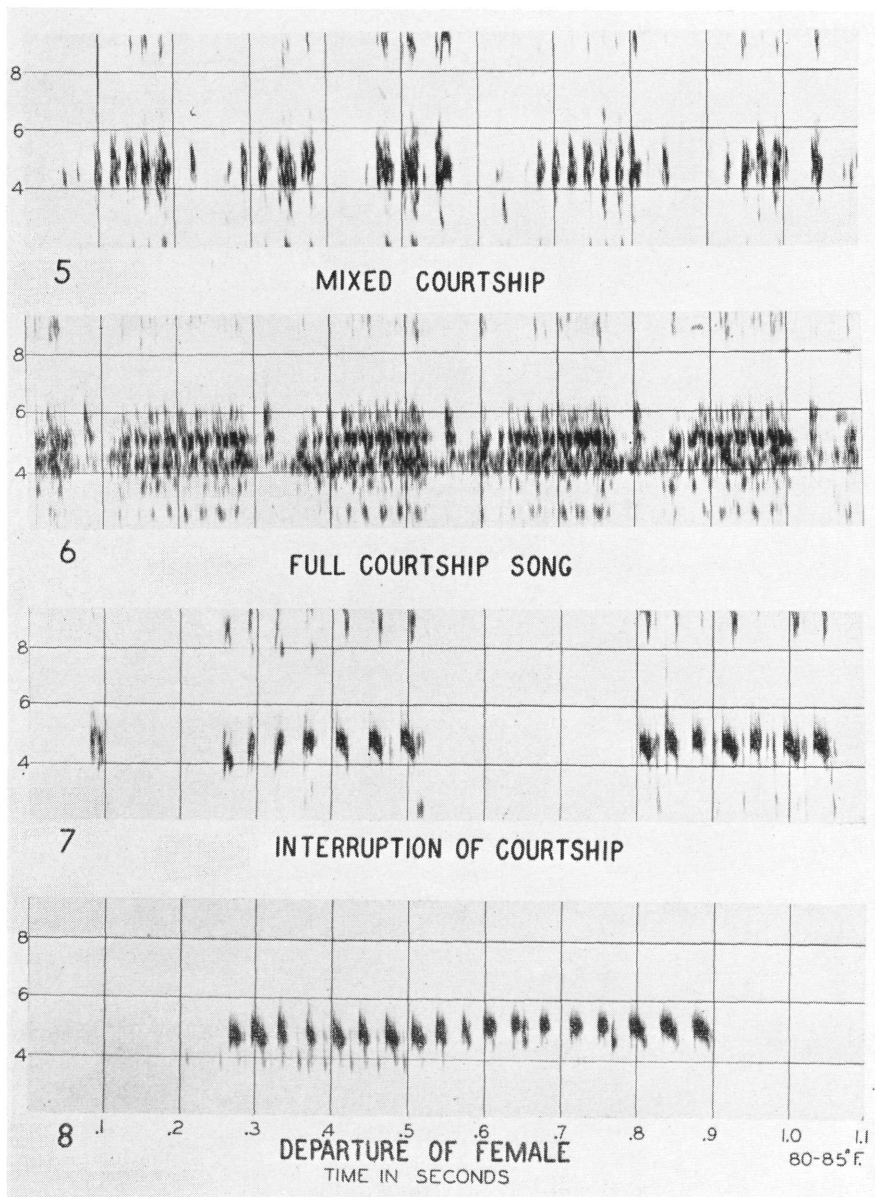
Magicicada septendecim (Linnaeus)⁴

(Homoptera: Cicadidae: Seventeen-Year Cicada)

The chief mechanism of sound production in cicadas is well-described by Pringle (1954). Two stiff, convex membranes (tymbals) at the base of the abdomen are alternately buckled inward by the contraction of a pair of large muscles attached to their inner edges, and popped back outward through their own resilience. This action may be compared to dimpling a plastic table tennis ball by pressing it with the thumb and then removing the thumb, thereby allowing the dimpled area to pop back to its normal shape. The drop in pitch near the end of the "Pharoah call" (congregational song, fig. 9) of the seventeen-year cicada corresponds to a lowering of the abdomen, which is slightly elevated during the rest of the call. In many cicadas rapid up-and-down motion of the abdomen provides a secondary pulsation which is superimposed on the more rapid rhythm due to the in-and-out popping of the tymbals.

Unlike the males of singing Orthoptera, male cicadas characteristically do not space themselves apart in the field and remain in one spot all their adult lives.

⁴These observations were made on Brood XIII during June, 1956, in DuPage County, Illinois.



The congregational songs of male seventeen-year cicadas are produced in series of 1 to 4 songs (rarely more), the insect flying a short distance after each series. Sometimes this flight between song series amounts to no more than a fluttering of the wings which may merely lift the individual from his perch momentarily, and at other times the male may fly several yards to another perch. Caged males rarely sing normally, since they usually strike the cage in these flights, and the rhythm of sing-fly-sing-fly is thus interrupted. Cicada behavior differs further from that of singing Orthoptera in that the males and females congregate into close proximity during the daily singing period. Often so many individuals are crowded together in a small tree or bush that the males are bumping each other continually while singing. Apparently no special male encounter sound has ever been heard in cicadas although on occasions when several males were gathered around a single female, a wing-flipping routine was noticed in which two or more of the males would alternately flip or flutter their wings briefly. This wing-flipping was also noticed in females apparently resisting courting males, and may have a relationship to the short bursts of wing motion between song series which usually result in flight. In some cicadas, a "wing-clacking" sound-producing mechanism occurs in both sexes (Myers, 1929; Pringle, 1954).

Courtship in the seventeen-year cicada consists of the male crawling on the back of the female, extruding his genitalia and moving them about on the ventral surface of the female's abdomen until he is dislodged or the genitalia are engaged. During this time he is producing a distinctive type of sound (fig. 10) which is somewhat analogous to the sound produced by courting male crickets.

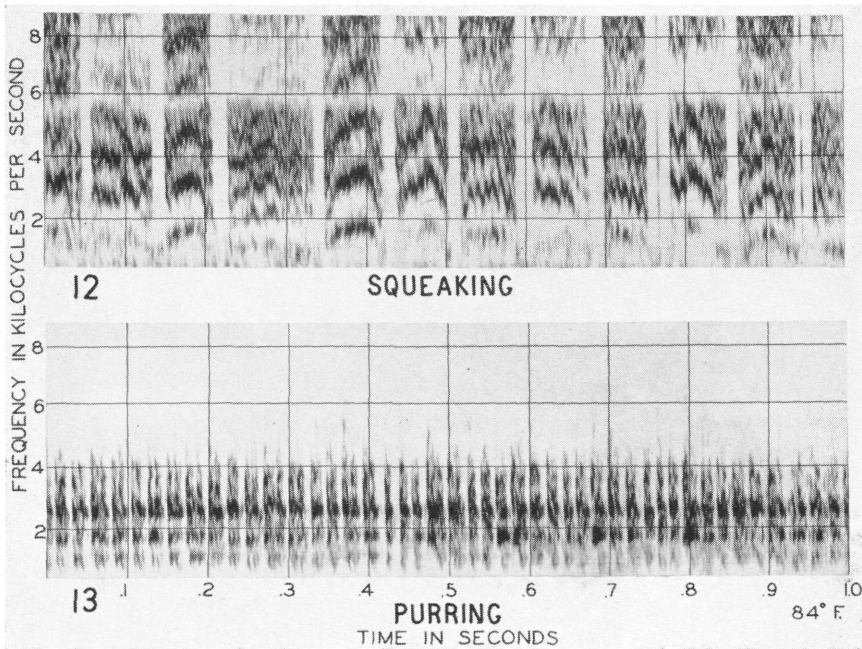
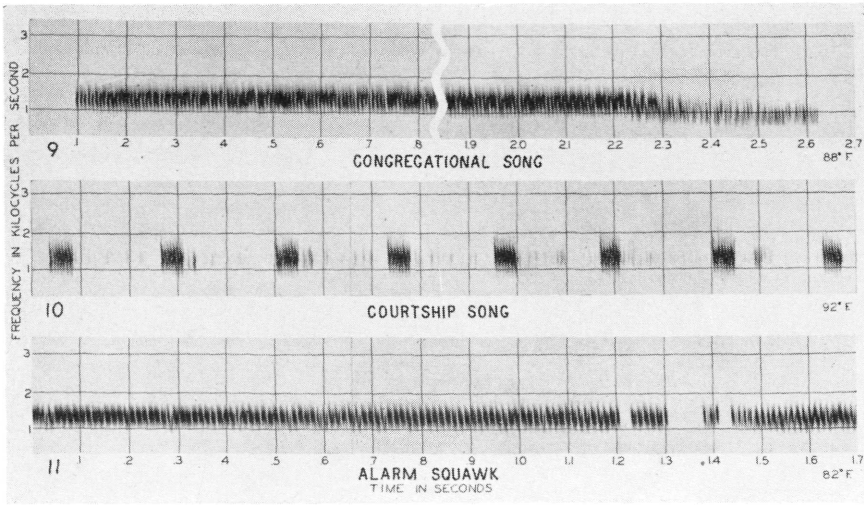
Male cicadas produce a third type of sound (fig. 11) when they are disturbed into flight, captured and held, pinched, poked, or otherwise manhandled. This sound is produced by male cicadas captured or chased by birds or cicada-killing wasps. Such "protesting" is known in only a few species of Orthoptera—*Amblycorypha oblongifolia* (DeGeer) (Blatchley, 1920), *Pterophylla camellifolia* (DeGeer), and *Neoconocephalus exiliscanorus* (Davis). It is the best-known sound in most small insects, such as beetles, bugs, caterpillars, leafhoppers, treehoppers, spittlebugs, ants, and velvet ants, probably because such insects are otherwise rarely observed in situations where their soft sounds can be heard.

The moving about by male cicadas during song and the congregation of large numbers of males into close proximity indicates that in cicadas a fundamental difference from orthopteran behavior is that individual females are usually not attracted to individual males by the congregational song. Rather, this sound draws large numbers of individuals of both sexes into close proximity and either the courtship song or some other stimulus is responsible for the pairing of individual males with individual females.

Tetraopes tetrophthalmus LeConte
(Coleoptera: Cerambycidae: Red Milkweed Beetle)

Relatively little attention has been paid to the sound-producing behavior of the thousands of species of beetles, ants, wasps, flies, moths, butterflies, leafhoppers, treehoppers, spittlebugs, true bugs, and many other small insects that are known either to produce soft sounds, or to possess specialized structures probably associated with sound production or perception. The sounds of most of these insects are so soft that they can be heard only if the insect is practically inside one's ear, or if some sort of amplifying device is set up (Ossiannilsson, 1949; Leston, 1955).

The red milkweed beetle was first noticed by the writer to make a sound when it was picked up and held. The noise made in this situation is a rather noticeable, shrill squeaking (fig. 12), produced by rubbing together stridulatory structures on the back of the pronotum and the front of the mesonotum. Several individuals



were taken into the laboratory and placed on the leaves and blossoms of milkweed (*Asclepias* sp.) in a quart jar. By listening at the mouth of this jar, one could hear a soft, almost continuous purring noise (fig. 13). A listening cage was set up by fitting a microphone connected to a tape recorder into a large rubber stopper, placing the stopper in a jar containing several beetles, and listening through earphones attached to the tape recorder which was turned to "record" position with the record gain turned up. The sound could be heard very clearly by this method while the beetles were being watched. Apparently both sounds are made by both sexes, and the situations in which they were observed are as follows:

1. When held
 - a. between the fingers (squeaking)
 - b. inside a closed fist (squeaking and purring)
2. When placed in a small cage
 - a. when moving about, or forcing the head down into cracks in corners of the cage (squeaking)
 - b. when standing motionless (purring)
3. When caught in a milkweed blossom (squeaking)
4. When placed or fallen on back (squeaking)
5. When fighting (one individual gripping some part of another with its mandibles (squeaking))
6. When two individuals meet and touch antennae or crawl over one another (squeaking or purring)
7. While undisturbed individuals are crawling about and feeding on milkweed leaves and blossoms (purring or squeaking)

Copulatory and pre-copulatory activities were watched several times, and the only time sound production was noticed was when the male was dislodged from the female's back, or the pair fell to the bottom of the jar from their perch on milkweed (squeaking).

It is evident, as already demonstrated by the investigations of Ossianneilsson on sound production in small Auchenorrhyncha (1946, 1949, 1953), that sound may play a complex part in the lives of small insects as well as in large species capable of producing intense sounds which carry great distances. The sounds of the red milkweed beetle are probably not intense enough to draw individuals together from outside the range of senses other than auditory. It is possible, however, that after the adults have assembled on milkweed, perhaps through olfactory attraction, the sounds cause further congregation or are involved in some phase of courtship or sexual selection. The observations recorded here are too scanty to allow more than speculation in this regard.

DISCUSSION

The high degree of differentiation between the sounds made by a given individual insect in different situations, and their consistency, suggests that the structural differences in these sounds are behaviorally significant. Likewise, the fact that no two species of insects, no matter how closely related, have been demonstrated to have inseparable calling or congregational songs, suggests the probability of discriminatory capacity. The writer has tape recordings of about 160 species of insects, representing six orders and fourteen families. All but a few of these can be distinguished by ear alone, and all can be separated by audio-spectrographic analysis. Included in this collection are recordings of several species which are as yet unrecognized by taxonomists because of the lack of observed morphological differences. When such closely related species are sympatric, their calling songs usually differ radically.

Additional observations indicate that structural differences in the calling songs of different species of insects may act as species isolating mechanisms. In the eastern United States, where hundreds of individuals in dozens of different species may be singing simultaneously in a small woodlot or marsh, inability of females to recognize the songs of males of their own species would result in utter confusion. Female tree crickets (*Oecanthus nigricornis* Walker) have been watched by the writer on weeds at night. In several cases the females were noticed to move only when a male two or three feet away on the same plant trilled. Yet, during continuous observations lasting a half hour to an hour, these females often moved only partway to the male, traversing practically every stem and leaf on the way, and moving only when the male trilled. If such a female responded equally to all insect sounds in the area, or even just to the most intense sound in her vicinity, her chances of meeting a male of the same species would be greatly reduced, and the time required would cause this to be a most inefficient communicatory system.

It is well-known that in many species of singing insects neighboring males synchronize or alternate the periodic elements of their songs. This phenomenon can be observed in the field even when such individuals are surrounded or intermixed with singing individuals of other species. Some of the night-singing Orthoptera begin singing in the evening when many species are already singing. When the first individuals begin to sing, the others in a colony chime in so quickly that dozens of individuals may be singing only a few seconds later. In some species, such as *Neoconocephalus nebrascensis* (Bruner), after the first individual in a colony begins to sing, the second individual starts out with his first phrase synchronized with that of the first individual, and each successive individual begins in synchrony with the chorus. This indicates that the near-simultaneous starting of song is not due entirely to a high and uniform degree of sensitivity to climatic condition, but rather to a response of one individual of a species to the beginning of song by another.

Even non-synchronizing species exhibit behavior that can only be explained by an ability to recognize their own sound. In species such as *Atlanticus testaceus* (Scudder), *Amblycorypha oblongifolia* (DeGeer), *Amblycorypha rotundifolia* (Scudder), and *Magisicada cassinii* (Fisher), the individuals do not sing continuously for long periods of time, but instead repeat their phrases only a few times, then are silent for a few minutes before singing again. In the field, different individuals of these species do not sing independently of each other, but rather a colony sings in bursts which are separated by intervals in which none or only a few individuals are singing. This means that these insects must be stimulated by their own sounds rather than by the hundreds of other, often more intense sounds around them.

The answer to the question of discrimination or lack of discrimination with respect to interspecific song differences may be reversed from one situation to the next. In localities where only a very few species are active in song at a given time of day or year, it seems likely that little selective value would be attached to a high degree of specificity to the particular details of structure in the sounds. However, in many species there are strong indications that relatively slight variations in rhythm or speed of pulsation in insect sounds are behaviorally significant.

SUMMARY

A large number and variety of insects produce sound with specialized apparatus. The chief structural variation in insect sounds, and the kind that is apparently behaviorally significant, is in the rhythm and rate of pulsation, or intensity modulation. In many species a variety of sound responses occurs in different situa-

tions, and no two species are known to produce identical sounds in the same situation. It is probable that song differences are important isolating mechanisms between closely related species of Orthoptera and Cicadidae.

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