Sound Communication In Orthoptera And Cicadidae [1, 2]

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COMMUNICATION can be said to occur whenever the activities of one animal influence the activities of another animal. Insects thus communicate in connection with all of the major classes of life activity, and they utilize all of the major communicative senses—visual, chemical, tactile, and auditory—in this communication. For purposes of the present discussion, communication among insects can be divided into short range signalling and long range signalling. Included in the first instance are situations in which the individuals involved are in close proximity, generally within range of more than one sense; and in the second instance, situations in which the individuals involved are relatively far apart and within range of a single sense only. Sound operates in both kinds of situations, but arthropod systems of sound communication have reached a high level of complexity and become diverse in function only when the initial assembly or coming-together of the adult males and females has become involved. In most insects this coming-together of the sexes is accomplished primarily as a result of 1) attraction of all the individuals to some feature of the environment (e.g., to a host plant or animal, or to ecological conditions existing only in restricted locations within the range of the species), or 2) the location and behavior of individuals of the previous generation (e.g., factors involved in determining the oviposition site of the females, particularly in species which mate upon emergence). In certain cases, however, communicative devices are known to be involved and to be effective over great distances. Riley (1895) demonstrated that a marked male of the *Ailanthus* silkworm moth, *Philosamia walkeri* Felder, could locate a female of the same species a mile and a half away during one night, apparently by the odor she emitted. More recent experiments reported by Collins and Potts (1932), Dufay (1957), Schwink (1958), and others have given

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[1] Manuscript received June 1959.

[2] Recordings illustrating this chapter are on Side I, Band 1 of the Demonstration Record.

similar results, showing that male Lepidoptera orient to the odor emitted by sexually responsive females from incredible distances. Travis (1939) found that males of the June beetle, *Phyllophaga lanceolata* (Say), orient to the odor emitted by the females at distances of 15 to 75 feet, depending upon the direction and velocity of the wind.

Visual stimuli operate at long range in the assembly of insects in several ways. Thus, Magnus (1958) found that size, motion, and color are involved in the male-female interactions in the fritillary butterfly, *Argynnis paphia* L., and Crane (1955) and Stride (1958) found that in other species of Lepidoptera the males first react to the females because of their color patterns or motions in flight. Downes (1958), Provost (1958), and others have shown that male Diptera assemble over "marker" objects and perform as groups when so assembled, probably stimulated both by the marker and by each other's individual activities. Such swarms attract the females, and mating frequently takes place within the swarm.

Buck (1935, 1937a, 1937b), Barber (1951), and others have demonstrated that males and females in the Lampyridae or fireflies (Coleoptera) are initially attracted to each other as a result of the light-flashing rhythms of the males, and in some species there is a sequence of interactions between the males and females which involves alternate flashing by both. This light-flashing system is remarkably analogous in many details to certain of the sound-signalling systems that have developed in the Orthoptera, as will be pointed out later.

Auditory stimuli have long been suspected to operate at long range in certain insects, chiefly because of the intensity and remarkably specific nature of song rhythms in sympatric species of Orthoptera and Cicadidae (Davis, 1928; Myers, 1929; Allard, 1929; Faber, 1929, 1932; Fulton, 1932; Pringle, 1954; Alexander, 1957b). Regen (1913) and Duijm and Van Oyen (1948) were among the first to show that the females of certain Orthoptera are attracted by the songs of males of their own species in the absence of other stimuli. Recent reviews by Pringle (1956), Alexander (1957a), and Frings and Frings (1958) have summarized the evidence for both long range and short range sound communication in insects. Information acquired since the publication of these reviews has primarily involved three systems which in terms of complexity, numbers of species, and broadness of the taxonomic categories involved, represent the major systems of sound communication in insects. These three systems are: 1) tegminal stridulation associated with tympanal auditory organs on the front tibiae in the Ensifera (Orthoptera: Saltatoria), 2) tegmino-femoral stridulation and alary crepitation associated with abdominal tympanal auditory organs in the Caelifera (Orthoptera: Saltatoria), and 3) tymbal vibration associated with abdominal tympanal auditory organs in the Auchenorrhyncha (Homoptera: Cicadidae and Cicadellidae). Walker (1957), Perdeck (1957), and Alexander and Moore (1958) have shown that the differences among the songs of sympatric species in each of these three groups are behaviorally significant and are involved in reproductive isolation among such species. The present discussion will be concerned with the significance of this and other new evidence detailing the operation of sound communication in these three groups.

ACKNOWLEDGMENTS

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THE OPERATION OF SOUND COMMUNICATION IN THE ORTHOPTERA AND CICADIDAE

In general, the sounds produced by Orthoptera and Cicadidae can be divided into five categories: 1) calling sounds by male[3], 2) calling sounds by females, 3) courtship sounds by males, 4) aggressive sounds by males, and 5) disturbance sounds by either sex or both. The first two of these sounds operate primarily at long range, the second two primarily at short range, and the last may be effective either at long range or at short range in the cases in which it operates as an intra-specific stimulus.

The conditions regulating production of these five kinds of sounds and their functions as communicative devices are diagrammed in Figures 1 and 2. The sequences indicated in Figure 1 are not to be interpreted as always suggesting cause-effect relationships, but primarily as descrip-

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[3] The variety of stimuli involved in evoking this sound, and its multiple effects, make it a difficult signal to label. The term "calling" has been selected from those in current use by various authors (common, ordinary, usual, spontaneous, indifferent, wonted, attracting, calling) because it is descriptive (implying "signalling," "summoning," "attracting," "drawing attention to by loud sounds," and "causing to assemble," according to various dictionaries), and it can be applied to a variety of species without undue presumption.

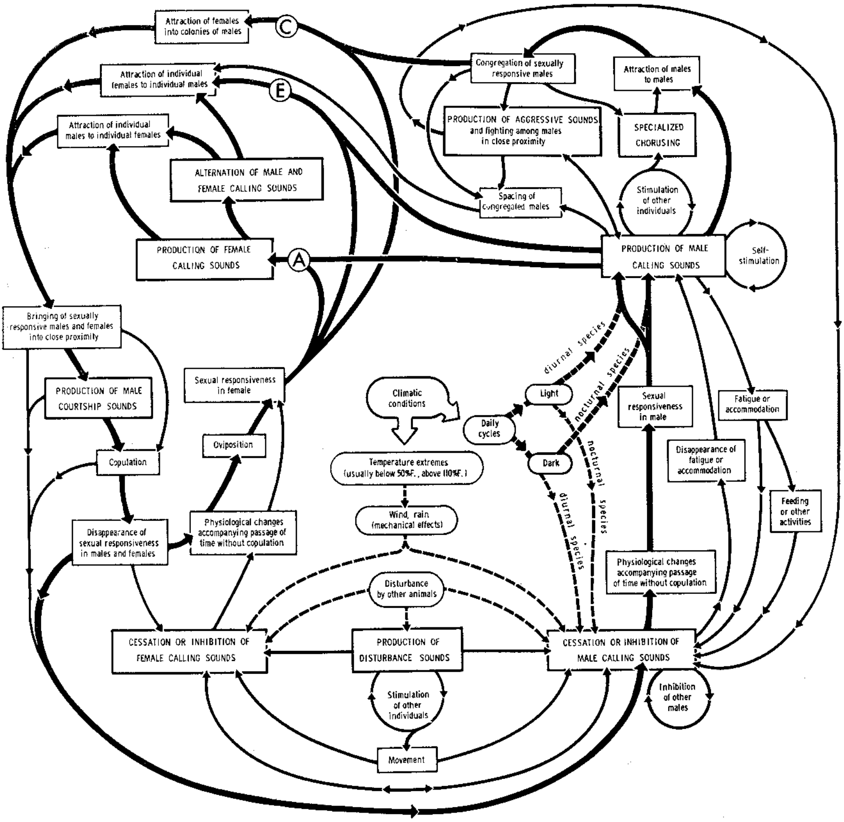
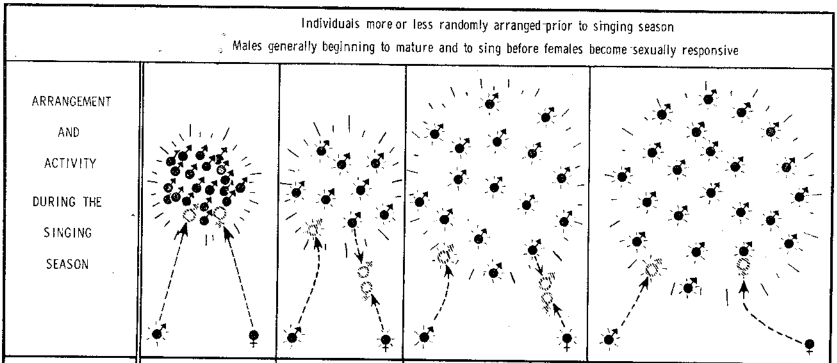


FIG. 1. A diagrammatic representation of the behavioral sequences and cycles associated with sound communication in adult Orthoptera and Cicadidae. Heavy lines indicate more important sequences, and the symbols (C), (E), and (A) designate sequences most characteristic of the Cicadidae, Ensifera, and Acridinae, respectively.

tive devices illustrating the sequences in which particular events ordinarily take place. The degree of completeness or incompleteness of available information with respect to particular portions of the diagram can be inferred from the specificity or lack of specificity in the terms employed.

Male Calling Sounds

As shown in Figure 1, these sounds are the only ones which are normally produced by individuals which are completely isolated from all others. Any sexually mature male in the three groups illustrated in



GROUP	CICADIDAE (most)	OEDIPODINAE	ACRIDINAE	TETTIGONIIDAE		GRYLLIDAE	CICADIDAE (few)
		(Acrididae)		(few)	(most)		
MALES SEDENTARY AND TERRITORIAL	no	sometimes	sometimes	sometimes	yes	yes	sometimes
CONGREGATE CHIEFLY BY	flying	flying and walking	walking	walking		walking	flying
TIME OF OPTIMAL CHORUSING	bright sunlight	bright sunlight	day	some, day some, night		night	day and dusk
VISION	very important	very important	important at close range	sometimes important		not important	probably not important
ECOLOGICAL LOCATION	vegetation	ground	ground	vegetation		ground or vegetation	vegetation
WITH DISTURBANCE SOUNDS	all	none	none	few		none	all

FIG. 2. A diagram illustrating the modes of assembly as a result of the calling songs in various Orthoptera and Cicadidae, and some correlations between behavioral and environmental phenomena.

Figure 1 can be expected to sing[4] at temperatures between 50° F and 110° F (approximately), provided that he 1) has not copulated recently, 2) is not disturbed by the presence of other animals or by the mechanical effects of wind or rain, 3) has not sung for a while, or has not been singing continually for a long period of time just previously, and 4) is located a) in the dark if a nocturnal species, b) in a situation of high light intensity if a diurnal species, and c) in a situation of low light intensity if a crepuscular species. All of these regulating factors combine to cause the males of each species to sing during definite, predictable periods of each day. Light intensity seems to be the most universally important single factor in determining the exact time on each day when different

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[4] Because the male calling sounds are rhythmical and repetitious, thus structurally resembling the "songs" of amphibians, birds, and humans (though lacking melody —characteristic of the last two named), they are commonly referred to as "songs," and an individual producing such a sound is said to be "singing." This usage will be employed here. The only other insect sounds known to possess these characteristics are the courtship sounds of various Orthoptera and Homoptera.

species begin song. Thus, most of the cicadas, meadow grasshoppers, band-winged grasshoppers, and slant-faced grasshoppers sing during the day, and certain species achieve optimal chorusing only in bright sunlight (Alexander and Moore, 1958). Some cicadas sing only at dusk for surprisingly brief and definite periods of time, usually less than one hour in length, as for example, *Tibicen auletes* (Germar) and *T. resonans* (Walker), sibling species occurring in eastern United States. When the light intensity has dropped to about five footcandles (estimated), these species begin to sing in chorus so suddenly that the noise of their starting resembles the sound of a great wind swelling across the woods. For a short period of time, cicadas seem to fly in every direction and the woods is literally alive with them. Then, as the light intensity continues to drop, the sound stops as suddenly as it began, at about the time when the chorus of night-singing Orthoptera is just beginning to develop.

Figure 3 shows the climatic conditions at the times when an isolated, dense colony of a nocturnal, coneheaded grasshopper began singing on several different evenings. Light intensity was the only factor in which there was no measurable difference from one evening to the next, except on two evenings when the mechanical effects of brisk rain delayed the beginning of song. Generally, the only other time that such finely tuned inhibition to light intensity as the triggering device in night-singing species is upset is late in the season when these insects are prevented from completing normal daily quotas of song by temperatures below 50° F from shortly after dusk until after dawn. Under these conditions the inhibition to light intensity is characteristically overcome earlier in the day, and many night-singers can be heard in middle and late afternoon, and rarely even at noon on the brightest days. Other factors may also enter in, such as the change in the ratio of daylight to dark, and changes in the quality and intensity of light during the daylight hours. Lutz (1932) has shown that there is a 24-hour cycle of activity in some Gryllidae and Tettigoniidae which persists for a time in the absence of the usual fluctuations in light intensity. It is likely that in some species the situation is similar to that demonstrated by Buck (1937a) in Lampyridae in which 24-hour cycles in the frequency of flashing by males of a nocturnal species, *Photinus pyralis* L., persist feebly even in continuous light or darkness, but relatively slight changes in light intensity cause increases in light flashing frequency at any time that they occur.

Although night-singing species begin at about the same light intensity from one evening to the next, their choruses generally dwindle noticeably after a few hours of darkness, and frequently one hears few or no individuals after midnight. Likewise, day-singing species generally stop chorusing, and sometimes stop singing entirely before the light intensity

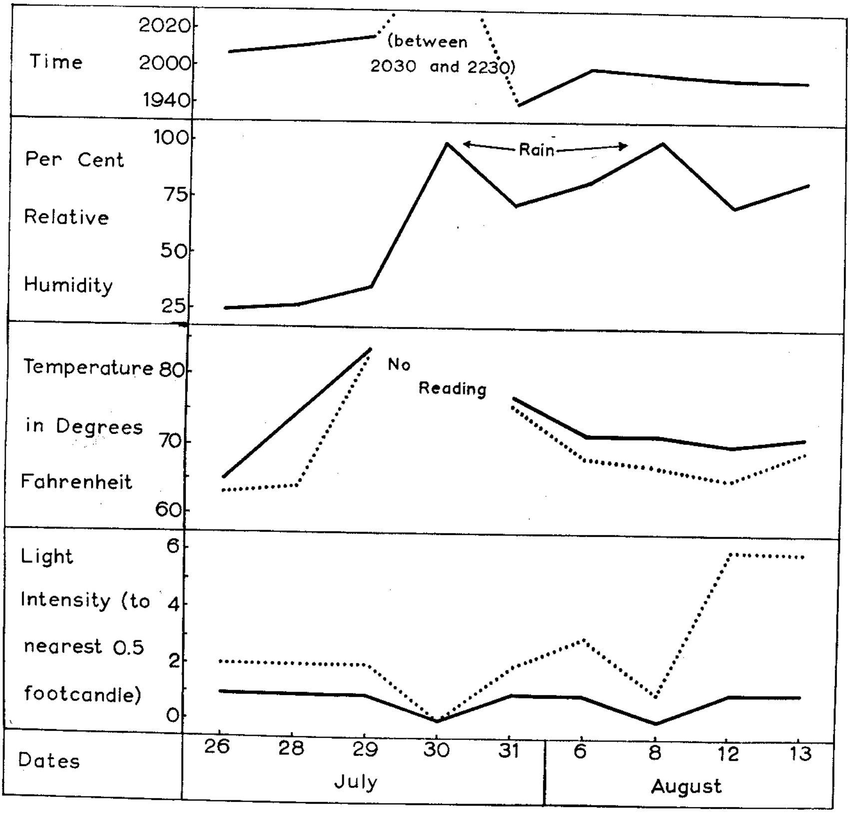


FIG. 3. Climatic conditions on several evenings at the time of beginning of song by an isolated, dense colony of *Neoconocephalus ensiger* (Harris) (Tettigoniidae: Copiphorinae). Dotted lines, in the open; solid lines, near the insects in vegetation.

has dropped to the same level that initiated singing. *Magicicada septendecim* (L.) begins to sing at dawn, and to chorus intensely when the first rays of the morning sun reach down into the trees, but only a few individuals are still singing in late afternoon when the sun is still high (Alexander and Moore, 1958 (Selection 2)). Part of this diminishment of singing volume is undoubtedly due to some of the males finding mates or becoming involved in courtship. Most of it, however, is due to an inability of the individual insects to maintain song during the entire period of the day that climatic conditions remain similar to those responsible for initiating singing (labelled "fatigue or accommodation" in Figure 1), and sound production is accordingly replaced by other activities. It is not unusual to see a male cricket which has been singing steadily for some time in the laboratory suddenly stop stridulating and begin to feed almost simultaneously upon food that was within reach when he began singing. Species such as *Tibicen auletes* and *T. resonans* operate somewhat differently in that individuals are probably able to participate continually in chorusing for a longer period of time than is represented by the proper climatic conditions during each 24-hour period. Whether the particular activity in species which operate within such brief daily periods is sound production, light-flashing, swarming in flight, or other behavior, the insects involved are nearly always crepuscular, and their level of activity is largely determined by changes in light intensity. Most often, such species are active in the evening rather than in the morning, and we can speculate that two advantages are involved: 1) fewer insectivorous birds are active, and 2) pairs entering into and remaining in copula for long periods of time are less vulnerable during the hours of darkness following dusk than they would be during the hours of daylight following dawn.

When cool nights or other disturbing factors prevent them from completing normal quotas of song, male Orthoptera sometimes sing under quite unusual conditions in addition to those already noted above. Thus, a male of *Acheta pennsylvanicus* (Burmeister), which I captured late in the season and was carrying inside my closed fist, produced a normal calling song there until dropped into a cage, where he began to sing again within two or three minutes. A male of *Conocephalus nemoralis* (Scudder) in early November produced a normal calling song almost uninterruptedly while dodging my hand as I made several attempts to capture him. A male of *Orchelimum vulgare* (Harris) sang almost continually for several days after remaining silent for a time in a small vial barely large enough to contain him which I carried in my pocket. A male of *Orchelimum silvaticum* McNeill was watched for several minutes singing normally while perched on a blossom eating a small bee which it had apparently just captured there.

The male calling song in Orthoptera and Cicadidae is the basis of the structure of sound communication in modern species; many of these insects possess no other sound signal. Directly and indirectly, the male calling song exerts many different influences upon the activities of both the males and the females in connection with the process of eventually bringing the adults into close proximity. When a male begins to sing, his sound affects his own behavior directly through the external auditory organs, continually restimulating him and setting the rate of production of certain of the rhythmical units in his song. There is evidence that male Orthoptera produce their rhythmical songs for long periods of time and with their usual precision only if their auditory organs are unimpaired. Deafened male field crickets which have never heard themselves or any other crickets, sing considerably less than nondeafened males and do not sing steadily for long periods of time as do normal males. This phenomenon will be discussed in more detail later when chorusing behavior is analyzed.

The calling song of the male likewise stimulates neighboring males, and males reared in isolation usually sing considerably less than males reared in groups. This has been reported by Haskell (1957) for Acridinae, and has been found to be true with field crickets in our laboratory.

Fulton (1928) showed that neighboring males of the snowy tree cricket, *Oecanthus niveus* (DeGeer), could not synchronize their chirps in chorus after they had been deafened. The starting in quick succession of many males in dense colonies, sometimes in synchrony with each other from the start (Alexander, 1957a), is relatively easy to observe in the field in eastern United States and is the chief reason that one can ascribe definite times of starting to entire colonies in order to make the kind of calculation shown in Figure 3. In the particular colony discussed here, beginning of steady singing by one individual always resulted in continued chorusing from that time, with a dozen or more individuals joining the chorus within a few seconds. There were never more than one or two very brief, irregular, and obviously abortive song starts prior to this time, and on most evenings there were none at all.

The assembly of sexually responsive males enhances chorusing behavior, which is more stable in dense colonies, thus operating as a feedback mechanism increasing the effectiveness of the colony as an attractant for outside males and females. The obvious formation of colonies of singing males in the field suggests strongly that the male calling song under certain circumstances (such as from a given distance or at a certain intensity) attracts other males. In most Orthoptera, lone males are generally less stationary than males which are incorporated into colonies, frequently shifting locations and singing from different perches on successive evenings. This is especially evident in long-winged individuals capable of flight. Alexander and Moore (1958) demonstrated in the field that the males of two species of 17-year cicadas are attracted by the songs of other males in the same species. Haskell (1957) found that male Acridinae sometimes orient and locomote toward speakers playing back the calling song of the species.

Some of the above effects of the male calling song upon the amount and kind of activity of other males, although suggested by field and laboratory observations, are yet to be clearly demonstrated in the Ensifera. Haskell (1953) failed to observe any reaction to the male calling song in caged male house crickets (*Acheta domesticus* L.), and none was clear in males of a California species of field cricket tested in our laboratory (Fig. 6) in a situation in which responses to both the calling song and the courtship song were obvious in females. More recent experiments have suggested that at certain times males respond to chirps from the calling song or to aggressive chirps by one or more of several activities, including 1) chirping aggressively once or a few times, 2) making short dashes, 3) flipping the antennae, or 4) pausing while locomoting (Alexander, Ms.). Adjustment of the rhythm of the sound by playing it at half speed or by increasing the speed by about fifty per cent nullified all response, suggesting that the particular sound of the species was the stimulus involved. No response to long-continued playbacks of steady chirping (calling song) has been evident.

As shown in Figure 2, in most Gryllidae and Tettigoniidae the males rarely move close enough together in the field to be within range of any sense other than hearing. They may remain this far apart through being repelled by each other's singing, though this has not been experimentally demonstrated. The males in these species are quite sedentary in such colonies, remaining within restricted localities and frequently returning to the same perch or burrow, and singing most often from that spot. In the laboratory, male field crickets become "attached" to introduced crevices or to burrows which they sometimes hollow out in the sand under objects. This occupation of crevices or burrows is characterized by several behavioral peculiarities: 1) restriction of the total area traversed by the occupying male, 2) long periods of time spent motionless in the crevice, 3) repeated movement in and out, and detailed examination of the crevice, 4) distinctive "sallies" outside the crevice at intervals, during which food and water are consumed and encountered males and females are fought and courted, respectively, 5) unusually direct returns to the crevice after being outside, 6) unusually aggressive reactions in encounters with other males, and 7) a decrease in the number of encounters with other males, frequently leading to virtual isolation for long periods of time. Such an occupying male is able to dominate encounters that he would lose under any other circumstances, and in one series of twelve encounters during five hours between two males occupying neighboring crevices, each male won all encounters near his own crevice and lost all encounters near the other male's crevice. Temporary isolation enhances the dominating ability of a male, thus working together in a reinforcing manner with territorial behavior in effecting the stability of natural colonies of male field crickets. A crevice-occupying male does not pursue males or females far from the crevice. However, temporary contact with other individuals frequently results in long-continued production of the calling song by a territorial male, by causing brief production of aggressive or courtship sounds through which the male is stimulated, either by external auditory feedback, some kind of internal feedback, or both, to keep chirping and gradually adjust into the calling rhythm. This response would have the desirable effect of calling back the departing female if she is sexually responsive, and possibly also of reinforcing the repellence of the temporarily contacted male. The conditions under which male field crickets are found in the field—permanently located at burrows or crevices, and spaced far enough apart to be within range of hearing only most of the time—seem to be those under which the calling song would be produced during a maximum amount of time and function most efficiently in guiding the sexually responsive females. An isolated male, once started into song, is less likely to be interrupted by outside disturbances than a male in a closely confined group or one in which the individuals are continually contacting each other.

In the Oedipodinae, the males move somewhat closer together than do the males of most Ensifera and Acridinae, within sight of each other, and they are less sedentary and less territorial. The formation of colonies of males interacting with each other and chorusing as a group in these insects is a day-to-day or even hour-to-hour phenomenon, as it is also in *Magicicada* spp., and the appearance of the same individuals in the same places in the same colonies from one day to the next is much less likely than in the Ensifera. Optimal chorusing seems to depend upon the males not only hearing, but seeing each other as well. In certain cicadas (e.g., *Magicicada* spp.), the adult males are drawn into compact masses by their singing, literally piling together and crawling over and around each other continually while chorusing. Both the Cicadidae and the Oedipodinae congregate chiefly through flying, and flying is actually a part of the chorusing rhythm in these insects, providing a visual stimulus along with the auditory stimulus involved (Isely, 1936; Alexander and Moore, 1958). Vision seems important in many aspects of the behavior of these insects which chorus optimally only in bright sunlight and are disturbed into flight by the movement of an observer several feet away. The band-winged grasshoppers (Oedipodinae) flash their brightly colored underwings during characteristic crepitating flights which are usually as distinctive and species-specific in the motion involved as they are in the sounds produced. For example, in the Carolina locust, *Dissosteira carolina* (L.), such a flight usually consists of taking off vertically, hovering while flashing the underwings and crepitating, then suddenly dropping back into the vegetation in almost the same spot from which the flight began. Cantrall (1943) describes the differences between crepitating flight, and flight after being flushed, in several species of Oedipodinae.

A set of observations made by the writer on the behavior of *Chortophaga viridifasciata* (De Geer) suggests how sound ordinarily operates in some species of Oedipodinae. As a result of alternate crepitating flights, three males assembled within a few minutes in a sparsely vegetated, gravelly area where they continued to fly and crepitate a few feet apart for several minutes without dispersing. Once during this time, two of the males landed about six inches apart, and one of them began to stridulate by rubbing his hind femora against the tegmina in the manner best known in the Acridinae. Stridulating intermittently, he moved to the other male by walking and taking short hops. Then he hopped and walked about the other male for about a minute, still stridulating, and occasionally moving his hind legs silently. Eventually the two males moved apart, and shortly afterward, the second male flew away without crepitating. A few minutes later, the first male crepitated, and a female flew into the area and landed about two feet away. Almost immediately, she began to stridulate tegmino-femorally and to walk and hop about. The male then walked toward the female, stridulated, walked again, mounted her, and copulated with her. The third male, meanwhile, had also approached the female, and he sat almost against the copulating pair, occasionally flipping his hind legs silently. This entire sequence took place in less than thirty minutes. All of the sounds were tape-recorded with the microphone inside a parabolic reflector about four feet away.

These observations reveal the close relationship between sound communication in the Oedipodinae and the Acridinae, and suggest that the systems utilized by the two groups had a common origin, probably in motions of the hind legs originally having only visual significance during courtship, or even earlier, only tactile significance after the male had mounted the female. Cantrall (personal communication) has observed that soundless stroking and flipping of the hind legs occurs characteristically in a wide variety of Acrididae during encounters between males and during encounters between males and females, both before and after the male has mounted the female. The crepitating flight of the Oedipodinae would appear to be an innovation utilizing sound, motion, and perhaps color in bringing sexually responsive individuals into ranges within which the tegmino-femoral stridulations can operate.

The spacing and behavior of the males in colonies of singing insects have a considerable effect upon the way in which the females are attracted. In the cicadas on the left side of the diagram in Figure 2, this is largely accomplished through an attraction of the females into very dense colonies of males, and the sound of the colony is more important for individuals outside the colony than the sound of any individual. Any differential mating in such instances must ordinarily take place with the female within courtship range of a number of males. In the Ensifera, on the other hand, in which the males are more widely spaced and more sedentary, individual females are probably most often attracted to within sight or touch of a single male without coming close to his singing neighbors, and the sound of the individual male is thus relatively more important for individuals outside the colony.

In the Ensifera and Acridinae the males and females congregate chiefly through walking. Vision is important at close range in the Acridinae, as demonstrated by Haskell (1958) who found that blinded females do not copulate. An additional significance for vision in the Acrididae is indicated by the fact that the males of most species take the initiative in courtship, leaping upon the female sometimes from a distance of several inches. In the Ensifera, in which the courting male simply backs under the female or allows her to mount upon his back, vision does not seem to be of much importance, even at close range. Optimal chorusing in most Ensifera occurs at night, and Khalifa (1950) found that the house cricket courts and copulates in total darkness with little or no delay. In the Ensifera the antennae are long, slender, active appendages which literally "trace out" the shape of objects encountered by the insects, while the antennae of Acrididae are short, thick, and much less active.

Although the basic function of the male's calling song is in every case the attraction of sexually responsive females, it seems likely that in most species these sounds actually have a greater variety of effects upon other males which hear them than upon the females. Thus, it appears that in different situations the singing of one male may cause another male to become more active, to become less active, to move toward him, to move away from him, to start singing, to stop singing, or to sing at a different rate or rhythm than he would if he were unable to hear the first male's song. In the Orthoptera and Cicadidae, elaboration of these different "side" effects would seem in every case to depend upon the ultimate enhancement of the primary function of bringing the sexes together, whether this enhancement operates directly or more or less indirectly through adjustments in the social organization of the species. It is possible that the variety and complexity of the effects of the calling song upon other males are responsible for the difficulty in making satisfying, positive demonstrations of function.

Male Aggressive Sounds

When sexually responsive males of the Ensifera are in close proximity, it is not unusual for them to exhibit aggressive behavior, frequently sparring or fighting with the antennae, forelegs, and mandibles, and kicking with the hind legs. Distinctive sounds are produced in this situation by many species, and there is evidence that these sounds affect the outcome of encounters between males, and are at least partially responsible for the later separation of the individuals. At the least, they are reflective of the aggressiveness of a male and his ability to dominate a particular encounter. Thus, when five adult male field crickets were placed together in our laboratory (Alexander, Ms.), the dominant male was the only cricket to chirp in 354 encounters occurring during the first three hours, and he produced aggressive chirps in all of the 223 encounters in which he was involved. The first male to chirp in an encounter with this dominant male later became dominant over him. In subsequent encounters, observed over a period of several weeks, the winning males chirped more often and usually produced more chirps than the loser in encounters in which both individuals chirped. The losing male rarely chirped after any kind of encounter; the winning male almost invariably chirped after combat. Sometimes this chirping immediately following a fight continued, the chirps gradually merging into the calling song, as noted earlier.

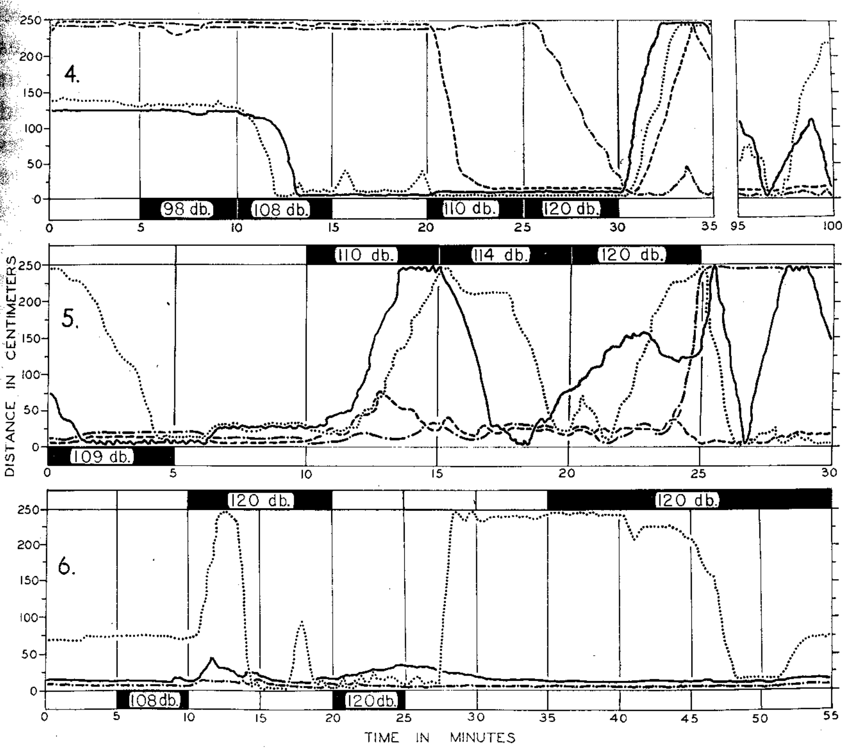
Female Calling Sounds

In the Gryllidae, and in most Tettigoniidae, the females are not known to produce any sounds which operate at long range, and in such cases the females simply move toward the singing males until contact is made through some sense other than auditory. In the Caelifera, and in a few Tettigoniidae, the females produce long range calling sounds upon hearing the songs of the males. The sounds of the male and female are usually alternated for some time, and the male may then move to the female, or both individuals may locomote (Figs. 1 and 2). Faber (1932, 1953), Jacobs (1953), Busnel and Loher (1954), Ragge (1955), Haskell (1958), Perdeck (1957), and others have discussed female calling sounds in European species of Acridinae and Oedipodinae, and Allard (1928) and Fulton (1933b) described such a sound for the katydid, *Microcentrum rhombifolium* (Saussure). In our laboratory a caged female of *M. rhombifolium* was noticed to be responding to the ticking song of a male caged nearby but out of sight. At the end of each series of ticks produced by the male, the female shuffled her tegmina, producing a brief lisp or tick that was so precisely timed with the male's tick-series that it seemed almost a part of his sound (Selection 4). Sometimes, immediately following this sound by the female, the male produced a curious, irregular shuffling sound. This sequence was observed and tape-recorded a number of times over a period of two or three weeks. Later we found that we could cause the female to make her sound and the male to follow with his shuffling noise by striking two razorblades together in imitation of the ticking sound of the male. Both Allard and Fulton noted that the males go to the females in this species when this alternation of sounds is taking place. The male of *M. rhombifolium,* apparently unlike any other Ensiferan, has two quite distinct sounds (Fig. 13) which are both produced by lone males. Possibly this species is similar to *Chortophaga viridifasciata,* the female locomoting toward the male as a result of one of his sounds, then producing a sound which stimulates him to produce his second sound and to locomote toward her. The similarity between the operation of the male and female calling sounds in *M. rhombifolium* and the operation of the male and female flashes in the firefly, *Photinus pyralis* L., is remarkable. In both cases the actual signals of the male and female are both nondescript, and it is their timing with respect to each other which carries significance (Buck, 1935).

Allard (1928, 1929) and Fulton (1933b) reported that females of other Tettigoniidae also produce soft, nondescript sounds which attract the males. Ordinarily, female calling sounds in both the Ensifera and Caelifera are produced only in response to the male calling sound. However, Ragge (1955) and Perdeck (1957) have reported instances in which female Acrididae produced sounds in the absence of the stimulation of the male's sound.

Male Courtship Sounds

Once the sexually responsive male and female are within range of some sense other than auditory, various courtship sequences are provoked, some involving the production of specialized sounds by the males. In the absence of outside disturbances or discordances in the interactions between the two individuals, copulation results. Demonstration of the actual significance of the specialized sounds produced by the males in this courtship sequence are even less extant than demonstrations of the functions of the calling sounds and aggressive sounds. Huber (1955) and von Hörmann-Heck (1957) believe that only the courtship song will cause females of *Gryllus bimaculatus* De Geer to assume the copulatory position. Ghouri and McFarlane (1957), on the other hand, found that female house crickets copulate with wingless males, and this has been confirmed in our laboratory by Mr. Kenneth C. Shaw. Perdeck (1957) and Haskell (1958) both found that silencing male Acridinae lowers the frequency of successful copulation with sexually responsive females with which they are caged in close proximity.



FIGS. 4–6. The effects of playbacks of the male calling and courtship songs upon adult male and female field crickets: Fig. 4—effect of the male calling song upon females; Fig. 5—effect of the male courtship song upon females; Fig. 6—effect of the male calling song (first 35 min.) and the male courtship song (last 20 min.) upon males. See text for further explanation.

In the Gryllinae, courtship singing involves a distinctive and elaborate motion of the tegmina, and it seems possible that the sound produced is most effective only when visual and possibly tactile stimuli are also involved. However, Khalifa's (1950) findings suggest that visual stimuli can be largely eliminated as a necessary factor in the courtship of house crickets.

Figures 4 and 5 show the difference in the responses of four females of a California species of field cricket (presently unrecognized, but near *Acheta pennsylvanicus*) to the calling and courtship sounds, respectively, of males of their own species played to them in the same situation. The females were placed in a cylindrical screen cage about 250 cm long and 10 cm in diameter—essentially a two-dimensional situation as far as direction of locomotion was concerned. A Jensen RP-302 super-tweeter attached to a Magnecord PT63A2HZ playback amplifier and a Magnecord PT63J tape-recording mechanism was then used to play continuous tape loops of the sounds shown in Figure 8. The speaker was located at one or the other of the ends of the cage, as indicated in Figures 4-6, and the ends of the cage were rounded so that the orientation of the females would not diminish as they approached the speaker. Intensities were measured at the point nearest to the speaker which could be reached by the females, using a General Radio Sound Level Meter, Type 1551-A, with an Amphenol Crystal Microphone, Model 9898. The cage was marked off into short lengths for ease of observation, and the movements of the caged insects were recorded at three-second intervals on especially prepared graph paper by two observers whose notations were timed and synchronized by a metronome in the background. The cage and the speaker were placed on thick cotton pads to reduce substrate vibration, and the observers stood behind a low wall to avoid disturbing the animals. The females used had all mated previously, but they had been isolated from males for 10 to 14 days previous to the tests. An important feature of this setup is that the females could orient directly toward the speaker from any part of the cage. Walker (1957) used a similar arrangement, but his rectangular cage was so constructed that the females could never orient directly toward the speaker, and if they moved toward the speaker along the screen surface of the cage, their angle of disorientation became progressively greater.

When observations were begun in each of the present experiments, the insects had been motionless for some time as is usually the case with this species during the daytime, and they were located in the positions shown on the left in each figure. The end of the cage ordinarily opposite the speaker was purposely made slightly darker than the speaker end so that the insects would be more likely to move to this end of the cage in the absence of other stimuli. Two of the females went to the dark end of the cage prior to the first test, the other two located near the center of the cage. When the calling song (Fig. 8) was played at 98 decibels, a slight increase in activity was apparent in the two females nearest the speaker. When the intensity was increased to 108 db, these two females immediately turned and walked quickly and directly to the speaker, and remained there as long as the sound was playing. A slight increase in activity was noted in the females at the far end of the cage during this part of the test, but they did not locomote until the intensity was increased to 110 db at the speaker end of the cage. At this time, one of the females oriented and walked directly to the speaker, stopping near the other two females. When the intensity was again increased, this time to 120 db, the fourth female came to the speaker. When the sound was shut off, all four females began to move away from the speaker. Their movement an hour later is shown, and the two less receptive females were less active at this time than the two receptive females. The intensities used here are all somewhat higher than those produced by singing males in this species. Several readings for calling and courting *Acheta* males of various species have given ranges of 70-100 db and 50-70 db, respectively, at a distance of about six inches.

Figure 5 shows what happened when the male courtship sound was played to the same females a day later in the same situation. This sound is normally produced only when males and females are in antennal contact, although it is frequently produced by males confined with other males, and even rarely by isolated males (Alexander, Ms.). In this test there was no stimulus available to the females other than the sound and that which their presence provided for each other.

The tests with the courtship sounds were also begun at a time when all of the females had been motionless for a considerable period of time. The less responsive females were located at the speaker end of the cage, one of the two more responsive females was near the speaker end of the cage, and the other was at the end opposite the speaker. When the courtship sound was played at 109 db near the speaker, both of the responsive females moved to the speaker, but without the obvious, quick orientation before starting to locomote, and not in the direct fashion of females responding to the calling song. These two females remained in the general area of the speaker, walking about, for five subsequent minutes when the sound was not playing. The speaker was then moved to the other end of the cage, and the same sound was played, this time at 110 db. All of the females became more active, and the two responsive females came to the speaker, though again they did not remain motionless near it as they had when the calling song was playing, but rather walked about erratically, eventually moving away from the speaker, and then starting to return when the intensity was increased to 120 db. The two less responsive females did not leave the end of the cage opposite the speaker. On two occasions the responding females exhibited a curious kind of behavior which was not noticed during the playing of the calling song or at any other time. When two females came into antennal contact during the playing of the courtship sound, they began to circle each other, each female playing her antennae over the back of the other (Fig. 7) in a manner closely resembling the behavior of a sexually responsive female approaching a courting male from behind. This peculiar behavior was continued for about a minute on both occasions that it was observed. When the sounds were finally discontinued, three of the females became inactive rather

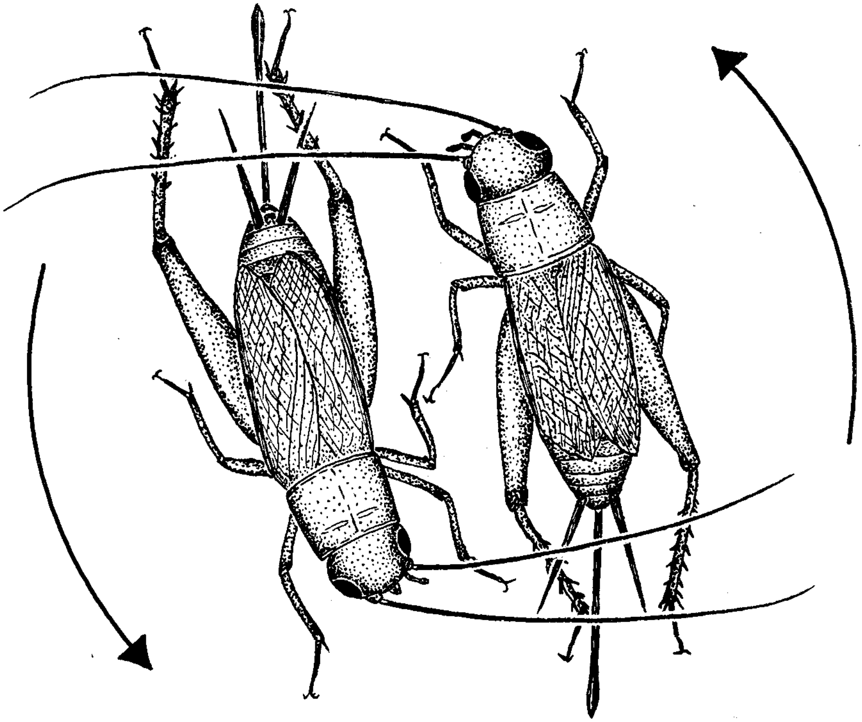


FIG. 7. Circling behavior of female field crickets coming into antennal contact while being stimulated by playbacks of the male courtship song.

quickly, while one female continued to move back and forth in the cage.

Several months after the above tests had been conducted, some unusual observations were made on the behavior of a single pair of field crickets caged alone, which shed light on the results obtained with the playbacks of the courtship sound to caged females. A male and a female of the F_1 hybrid generation from a cross between an *Acheta firmus* (Scudder) male and an unidentified *Acheta* female (pale brown with a striped head, collected on the beach on Grand Isle, Louisiana) were placed together in a cage on the writer's desk with the primary intent of securing eggs to continue the culture. Both individuals had been caged in isolation since maturing. The male had never been observed to stridulate before this time. Upon contact with the female he began to chirp, and to orient his rear end toward the female's head. The female responded to antennal contact with the male by becoming immobile. Each time the male chirped, the female moved forward in the usual manner of sexually responsive females in the presence of courting

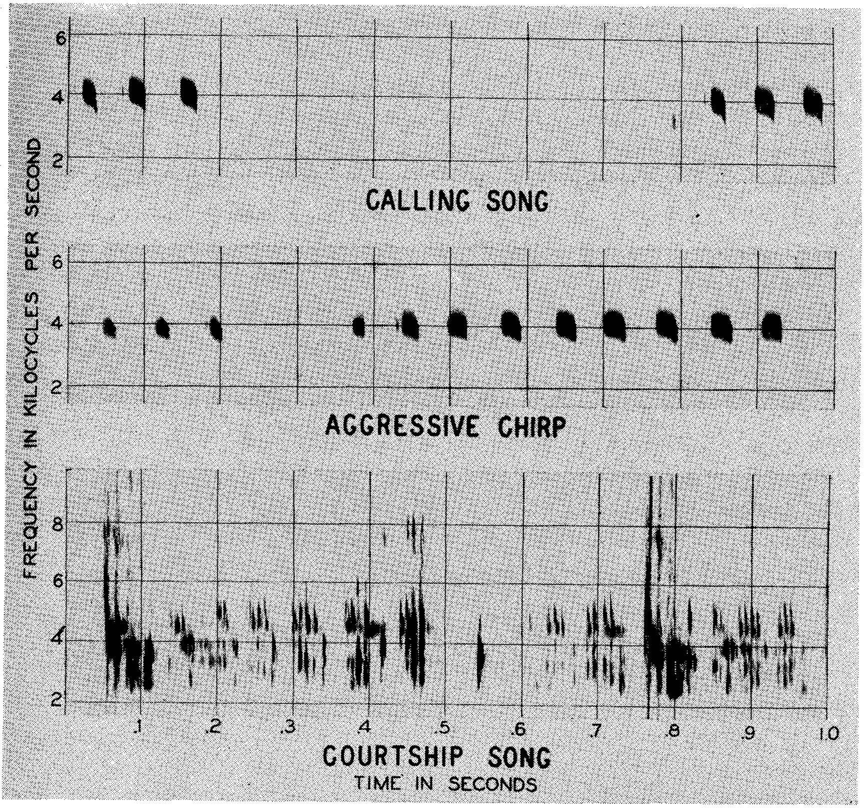


FIG. 8. The three basic sound signals of field crickets, illustrated by spectrograms of tape recordings of *Acheta firmus* (Scudder) (2nd generation reared adults from Grand Isle, Louisiana).

males, and had there been no discordance, she presumably would have mounted and copulated with him. However, the male's chirping was each time brief, and the female's approach was an abrupt jerk forward against him. The result was that each time the pair came into contact, the male oriented, chirped one or twice (not continually, as is usual in *Acheta*), the female jerked forward immediately, and he jerked away at her touch. In 74 consecutive initiations of courtship in this fashion, the female was immobile when the male chirped, she jerked forward at his chirp, and he jerked away if she touched him, or ceased chirping if she did not. Several times the female left the male after such an encounter, and when he chirped next, she was several inches away, twice behind the water vial out of sight and several times facing directly away from the male or at an angle away from him. Nevertheless, each time he chirped, within about one tenth of a second she dashed forward, regardless of the direction she was facing. After 74 such responses, observed over a period of two days, the female walked up on the male's back for the first time, and although she fell off this time without the spermatophore being attached, she immediately remounted the male and successful copulation occurred. Thereafter the male produced the courtship sound progressively more perfectly and continuously, and the courtships and copulations were comparable with those usually observed.

This unusual opportunity positively confirmed that the courtship sound alone can cause forward locomotion on the part of a responsive female. This forward movement results in the female mounting any individual which happens to be in front of her, or at least leads into the mounting act. Together with the results obtained with playbacks of the courtship sound, these observations suggest that the courtship sound in field crickets does not possess the characteristics of the calling song which make the latter a highly directional stimulus, but that it does have certain unique effects upon the female which increase the likelihood that she will assume the copulatory position and shorten the length of time involved in pre-copulatory maneuvers.

It should be noted that the above results, while in agreement with the conclusions of Huber (1955) and von Hörmann-Heck (1957) concerning European field crickets, are at variance with results obtained by Haskell (1953) with the house cricket. Haskell suggests that in this species, the calling song causes short bursts of locomotor activity and the courtship sound causes cessation of locomotor activity. He does not fully explain how these determinations were made, and it seems unlikely that such a great difference exists between species in the same genus which otherwise behave similarly in most respects.

As with the calling songs, there are occasionally species with two or three different male courtship sounds, each characteristic of a particular stage of courtship (Alexander, 1957a; Alexander and Moore, 1958; Alexander and Thomas, 1959). In crickets the structural changes in the sound produced during the courtship sequence are usually so gradual that one cannot separate the sounds produced into separate entities, but must consider the entire sequence more or less as a unit. This is well illustrated in the sequence of courtship sounds of *Acheta pennsylvanicus* in Selection 1 (See Alexander, 1957a, for spectrograms).

Immediately following copulation, neither the male nor the female produce calling sounds and neither engages in copulation again for periods of time which vary from a few minutes in some crickets to until oviposition has been accomplished in the Acridinae (Haskell, 1958).

Even in crickets, if the female does not find suitable ovipositing substrate she ceases to copulate after a few days, although she may copulate several times without ovipositing. With the passage of time, and with oviposition of the female, the males and females again become sexually responsive and the cycle involving sound production and specific responses to it begins again. It seems likely that in none of the singing Orthoptera or Cicadidae is a single copulation per female or per male the rule. Field crickets copulate repeatedly at intervals of a few minutes if undisturbed, and on several occasions I have seen male field crickets successfully initiate copulation with a female while one or two spermatophores from previous copulations were still attached to her. In such cases the old spermatophore is either pushed out of the way by the male as he attaches the new spermatophore, or the female pauses after mounting the male with the old spermatophore obviously impeding attachment of the new one, and rubs the old spermatophore off with her hind legs or bites it off with her mandibles.

Disturbance Sounds

Most species of Cicadidae and a few Orthoptera produce characteristic sounds when they are restrained, startled, or otherwise disturbed, generally by visual or tactile stimuli produced as a result of the activities of other animals. Apparently, the production of such sounds, as well as the cessation of production of the calling song by nearby males as a result of disturbance, can through auditory stimulation alone cause other individuals to cease production of the calling song. Almost anyone who has collected Orthoptera or Cicadidae by tracing individual singing males has had the experience of all the singers in an area stopping abruptly when the first individual was captured and silenced or caused to produce the characteristic squawk of restrained individuals of the species. In *Magicicada cassinii* (Fisher), causing one individual to squawk during times when the light intensity is slightly below the chorusing threshold, results in brief production of the calling song by nearby individuals, and this may be reinforced until a large group choruses for several minutes before the sound again dwindles away. It seems at times that causing a single male cicada to fly and to emit the disturbance squawk is the direct cause of an entire treeful taking off and squawking in chain reaction. Whether the stimulus here is visual, auditory, or both remains to be discovered through careful experimentation.

Most male cicadas produce disturbance sounds, and it seems likely that all of the sounds produced by tymbal vibration in cicadas had an origin in sounds produced in this situation. In the Ensifera, on the other hand, there is good evidence that the sound-producing and auditory structures both arose in connection with courtship, and that disturbance sounds in the few species possessing them are secondary. It is interesting that among the Orthoptera, only species which live and sing on vegetation produce disturbance sounds, and in the different species the possession of this response does not seem to be of common origin. Of approximately fifty species of Gryllidae and ninety species of Tettigoniidae tape-recorded and handled by the writer, only the following four species of Tettigoniidae have been observed to produce this response: *Neoconocephalus exiliscanorus* (Davis) (Copiphorinae), *Aglaothorax armiger* Rehn and Hebard (Decticinae), *Pterophylla camellifolia* (Fabricius) and *Liparoscelis nigrispina* Stal (Pseudophyllinae). Only a few individuals of the first species named have produced this sound when handled, but they did so readily and for several seconds continuously each time. The last three species are all large, flightless, slow-moving, sedentary night-singers, suggesting a possible correlation with susceptibility to predation.

THE IMPORTANCE OF RHYTHM PATTERN IN INSECT SOUNDS

The most important parts of the structure of insect sounds, in terms of specific effects upon the behavior of individuals which hear them, are their rhythm patterns (Walker, 1957; Perdeck, 1957; Haskell, 1958; Alexander and Moore, 1958). Examination of all the different kinds of sounds known to be produced by insects reveals that the male calling songs are the most intense, the most distinctive, the most rhythmical, the most complex, and the most long-continued of all insect sounds. This is not surprising if we consider the kinds of selective forces that must have been acting upon them as a result of the fact that they operate at great distances and generally represent the initial contact between adult males and females. Increases in intensity have probably been generally favored because they increase the range and thus the effectiveness of the sounds in the assembling function. Increases in the amount of time spent in song by individual males and the development of specificity with respect to the time of day or night that the males of particular species sing and the females are responsive also increase the chances that the two sexes will get together. In groups in which individual males (rather than choruses) attract individual females, selection should operate primarily in increasing the total amount of time spent in song by individual males. Thus, the success of a sedentary, territorial, relatively isolated male of an ensiferan species in attracting females (and thus transmitting genetic material to subsequent generations) depends largely upon his prowess as an individual singer. Not only the rhythm pattern and intensity of his song are important, but also the amount of time that he can produce the song during particular parts of each 24-hour period. In groups in which the attractive function primarily involves the singing behavior of the colony (chorus) rather than the singing behavior of individual males, it is most important that the individuals become synchronized with each other in terms of the daily singing period. This has been effected primarily through 1) increased specificity to daily cycles of light intensity, and 2) increased sensitivity to sound production and other activities of the other individuals in the species (such as flying as a part of the singing rhythm in *Magicicada* spp.). The culmination of this trend, illustrated by *Tibicen auletes* and *T. resonans,* has resulted in a very much shortened daily period of song, but one in which nearly every individual becomes active at the same time. In these species, the success of an individual male depends largely upon his ability to conform and thus become a part of the colony. The male most likely to copulate is one which reacts to changes in light intensity and other climatic conditions, and to the other males, in the same way that the other males react to climatic conditions and to each other.

If more than one species lives in a particular area, one would expect a selective advantage to be attached to the development of structural differences in the songs of different species and to a corresponding specificity of response in the females. Any increase in the number of sympatric species utilizing sound as a primary assembling mechanism in a particular area, owing to this pressure for divergence in song patterns, should result eventually in a trend toward greater complexity, causing an increase in the number of potentially significant structural features. The kind of song possessed by a particular species would then depend chiefly upon two aspects of its history: 1) the kind of song possessed by its immediate ancestor (and the limitations imposed by the kind of apparatus acquired through heredity), and 2) the sound environment in which it has developed as a species. Since most of the intense selection should operate with respect to the calling song, we should expect that the structure of other sound responses possessed by the species would be more or less reflective of the structure of the calling song. All of these suppositions appear to be correct, and because of this, any reconstruction of the evolution of structure in insect sounds is most profitably centered around the male calling songs. As might be expected, parallel evolution in song rhythm patterns seems to have taken place in different sound environments—geographic areas within which all of the singing species are directly or indirectly interacting with one another and have been during most or all of their history as sound-communicating species. For example, although I am not apt to confuse the songs of different species of cicadas in eastern United States with each other, I did confuse the songs of Ceylonese cicadas recorded by J. W. S. Pringle with those of some of the species occurring in eastern United States before becoming aware that the sounds I was hearing were not the songs of cicadas from eastern United States. Certain of the songs of Mexican and southwestern United States Orthoptera form close parallels in rhythm pattern with the songs of more or less unrelated species in eastern United States with which they are allopatric and have been for thousands of years. As further evidence of the fact that the evolution of rhythm patterns in the calling songs has proceeded more or less independently in different geographic areas, one can locate the entire range of structural complexity in insect sounds—from the simplest possible patterns, almost non-rhythmical, to the most complex ones known in the world—in the calling songs of the 250 or so species of singing Orthoptera and Cicadidae in eastern United States. The publication of comparative studies of the sounds of all the species living together in different geographic areas of the world is a desirable undertaking which would be of considerable value to those interested in the evolution of communicative mechanisms. Such studies should include not only the structure of the sounds, but also degrees of sympatry among species, both in terms of macro- and micro-distribution, and in terms of seasonal and daily singing periods. No such comparative study has yet appeared for any region, utilizing modern recording and analyzing equipment in the descriptive aspects. The studies of Fulton (1932, 1951), Faber (1929, 1932, 1953), Pierce (1948), and Pringle (1955) are contributions in this direction (See also, Alexander and Borror, 1956).

Most insects are able to deliver not just one but a number of rhythms in their different sound responses, as is well illustrated in the subtle modifications in the sounds of *Acheta pennsylvanicus* and in the repertoires of other species accompanying this paper. The basic rhythm in all insect sounds, including the different sounds in the repertoires of single species, is a pulse rate depending upon the rate of oscillation or vibration of the sound-producing apparatus—the tymbals in cicadas, the tegmina in Ensifera, and the tegmino-femoral and alary apparatus in Caelifera. The pulse in an insect's sound may be considered comparable to the "phoneme" in human language (Hockett, this publication). Thus a single pulse is in most cases meaningless, and pulse-groups of different lengths and patterns have differences in their significance. Most insect "languages" possess only a single phoneme, but in the courtship song of Gryllinae (Fig. 8) there are variations in intensity and uniformity within the pulses and also in the spacing of pulses which suggests that it would be more accurate to speak of two or three different kinds of phonemes. Let us consider the first two field cricket sounds shown in Figure 8 in terms of their structural relationships and their specific effects upon the females.

The calling song of a chirping field cricket contains one kind of pulse or phoneme and one morpheme—the multi-pulse chirp. This sound affects the behavior of a sexually responsive female in the following respects: 1) she orients toward the source with a high degree of accuracy, and 2) she locomotes steadily in a fairly straight line (if there are no obstructions) toward the source of the sound. There may be other effects, but these have not been demonstrated. The courtship song differs from the calling song in the following respects: 1) the dominant frequency is lost and each pulse is less intense and more "ragged"—less obviously a single, intense unit (transient), 2) each pulse group contains about twice as many pulses delivered at about twice the rate as compared with the calling song, probably because in the courtship song the stridulatory apparatus is engaged during both the opening and the closing of the tegmina but only during the closing in the calling song, and 3) between the pulse groups there occurs a distinctive, intense, single pulse, slightly separated from the others. This courtship song affects the behavior of a sexually responsive female in the following respects: 1) she locomotes in short, irregular dashes forward, 2) she orients to the touch of another individual and walks up on that individual if possible.

These lists of effects are probably both incomplete and improperly categorized. Thus, a female approaching a calling male might also mount more readily than she would upon a silent male, but this situation would be difficult to produce since a calling male begins to court upon contact. On the other hand, the females in the test described earlier (Fig. 4) became motionless in the area of greatest intensity of the calling song, suggesting that a female touching a calling male might in some circumstances remain immobile in contact with him until he began courting. This response, whether by a male, a female, or a nymph, induces courtship in a calling male.

In the list of effects suggested above, the chief variation in the reaction of the female is her ability to orient directionally to the source of the calling song with a high degree of accuracy. Likewise, in comparing the structure of the two sounds it is obvious that the chief difference which separates the calling song from the softer, creakier, more nondescript courtship song is the superimposition of discreteness in the character of the pulses and the pulse intervals. The evolution of an increasing ability to produce intense, clear chirps not only increased the male's range of effectiveness, but also introduced characteristics which allowed the increasingly sensitive auditory organs of the female to become more effectively directional at a greater distance.

One obvious structural difference between the courtship and calling songs illustrated in Figure 8 remains totally unexplained. The courtship song actually possesses two kinds of pulses or phonemes—the ordinary, less distinctive pulse produced in groups, and the distinctive, isolated pulse produced between groups. What is the significance of the rhythm created by the introduction of this distinctive pulse? It appears gradually as the male changes to the courtship song, and it occurs regularly only after the rhythm has been fully developed. In chirping species, the rate of delivery of this lone pulse sometimes corresponds to the rate of delivery of the chirps or pulse groups in the calling song. Without it there would be no characteristic in the courtship song comparable to the chirp rate in the calling song, since the pulse groups frequently run together and are never as discrete as in the calling song. Unfortunately, we do not yet know the significance of the chirp rate in field crickets, although it is usually species-specific with some overlap between species. Walker (1957) showed that the chirp rate, in the calling song of the tree cricket, *Oecanthus niveus*, is significant. The females responded to pulseless, artificial "chirps," but not as well as they did to the natural, pulsed chirps, and they failed to respond at all to continuous trills in which the pulse rate was identical to that in the chirp. However, the distinctive pulse described above is sometimes as evident in the courtship of trilling field crickets as in the courtship of chirpers.

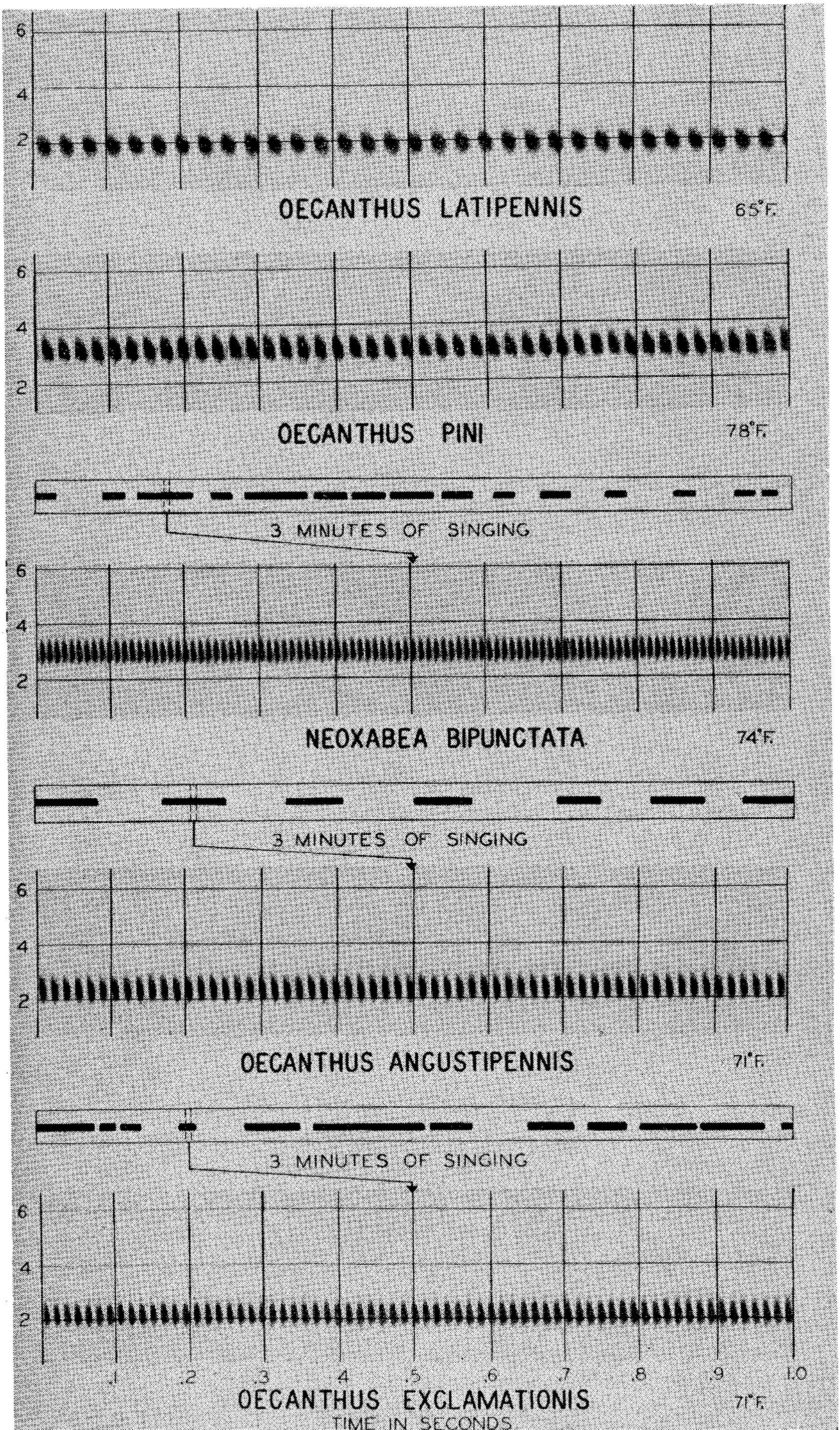
There is obviously much to be learned concerning the significance of subtle modifications and differences in the sound "languages" of crickets, which may be considerably more complex and varied in their specific functions than we have been able to demonstrate thus far.

THE EVOLUTION OF RHYTHM IN CALLING SONGS

A cursory survey of the rhythm structure in the calling songs of several species of Orthoptera and Cicadidae will give some idea of the kinds of patterns which are significant, and of how complex patterns have evolved from simpler ones.

Simple succession of oscillations of the sound-producing apparatus

FIG. 9. The calling songs of five species of tree crickets (Oecanthinae), illustrating simple trills—continuous in the first two species and broken in the last three species. Top to bottom: Franklin Co. O., 21 Sept. 1954; Raleigh, N. C., 8 Aug. 1955; Franklin Co. O., 28 July 1954; Franklin Co. O., 23 Aug. 1954; Franklin Co. O., 28 July 1954. (Ordinate, kc/sec.).

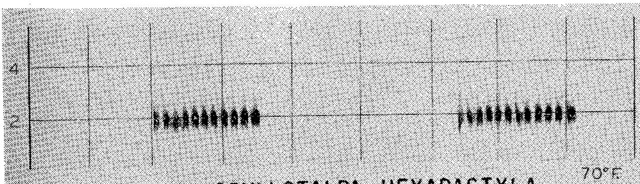

6
4
2
OECANTHUS LATIPENNIS
65°F.
6
4
2
OECANTHUS PINI
78°F.
3 MINUTES OF SINGING
6
4
2
NEOXABEA BIPUNCTATA
74°F.
3 MINUTES OF SINGING
6
4
2
OECANTHUS ANGUSTIPENNIS
71°F.
3 MINUTES OF SINGING
6
4
2
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
OECANTHUS EXCLAMATIONIS
71°F.
TIME IN SECONDS

result in simple "trills" such as those illustrated by the songs of several species of tree crickets in Figure 9. These sounds contain but a single rhythm element of sufficient uniformity to be considered potentially of much behavioral significance, and this is the basic pulse rate. As shown in Figure 9, differences in pulse rate are the chief interspecific variables in this type of song. Successions of pulses may be produced more or less continually as in the songs of *Oecanthus latipennis* Riley and *O. pini* Beutenmuller, or in bursts of irregular length and spacing as in the other three species illustrated, without changing the fundamental nature of the sound. Walker (1957) found that females of species with irregularly broken trills responded as well to continuous trills as to broken trills. These trills represent the simplest and most common kind of calling song occurring in both Orthoptera and Cicadidae.

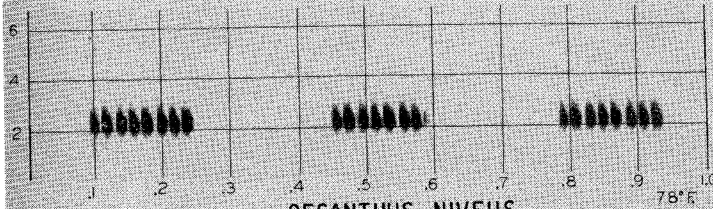
The calling song of *Acheta pennsylvanicus* (Selection 1) and the *Acheta* calling song illustrated in Figure 8 are chirping songs, representing the next step in evolution toward greater complexity in rhythm pattern. Figure 10 illustrates chirping songs of species in the six subfamilies of crickets found in eastern United States. In these songs behavioral significance could possibly be attached not only to the pulse rate, but also to the chirp rate, to the length of the chirp relative to the length of the chirp interval, or even to the regularity of the chirp interval. Thus, the number of potentially significant characters has tripled or quadrupled with this simple change of making the length and spacing of pulse groups more uniform. The songs in Figure 10 can also be distinguished from one another on the basis of characteristics which are probably of little importance to the insects themselves, such as frequency or cycles per second (in crickets the dominant frequency corresponds to the number of teeth of the stridulatory vein struck per second), and structure (e.g., number of toothstrikes) in the individual pulses. Some of the katydid songs illustrated in Figure 12 are made up of similar, simple groupings of pulses.

Progressing toward increasing complexity, we can find songs in which the pulse groups themselves are grouped, as in the three songs illustrated in Figure 11. In these songs there are interspecific differences in the length of the pulse groups, in the length of the secondary groupings, and in the pulse rate. Again the number of characteristics of potential behavioral significance has increased.

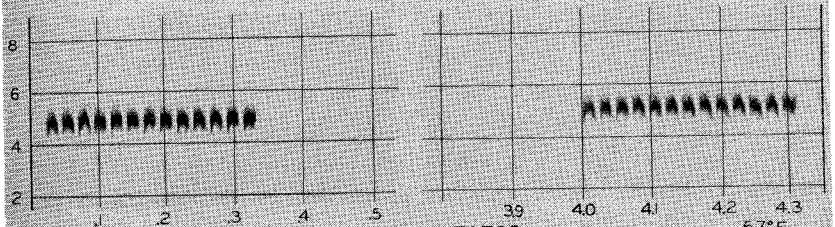
FIG. 10. Chirping, calling songs in six different subfamilies of crickets. Top to bottom: *Gryllotalpinae,* Champaign Co. O., 24 Aug. 1954; *Oecanthinae,* Erie Co. O., 26 July 1955; *Eneopterinae,* Dyar Co. Tenn., 24 Sept. 1955; *Gryllinae,* Florida laboratory culture; *Trigonidiinae,* Lenoir, N. C., 2 Aug. 1955; *Mogoplistinae,* Raleigh, N. C., 8 Aug. 1955. (Ordinate, kc/sec.).



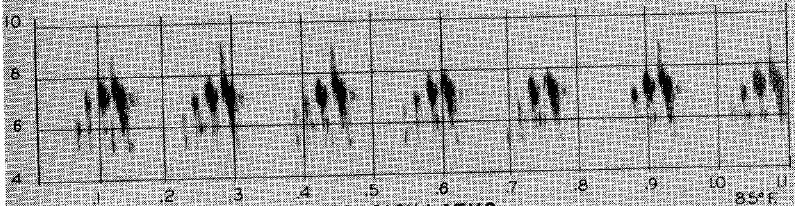
CRYLLOTALPA HEXADACTYLA



OECANTHUS NIVEUS

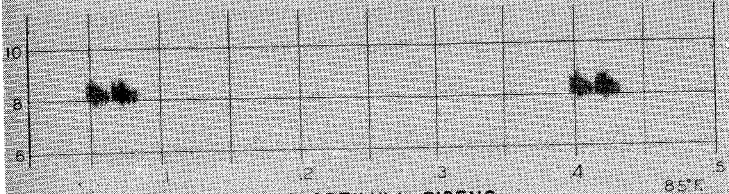


OROCHARIS SALTATOR



GRYLLODES SIGILLATUS

CYRTOXIPHA COLUMBIANA



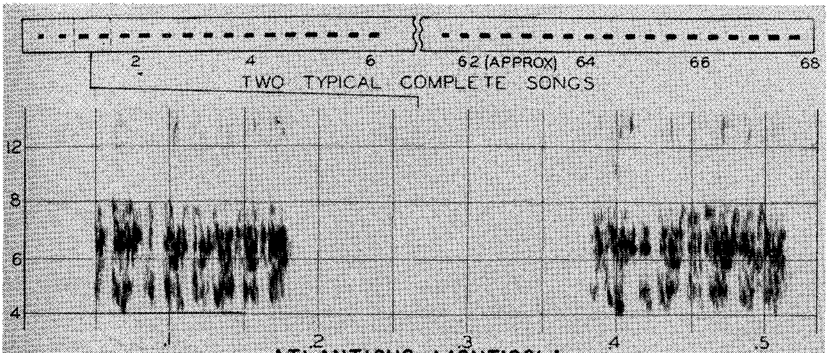
CYCLOPTILUM BIDENS

TIME IN SECONDS

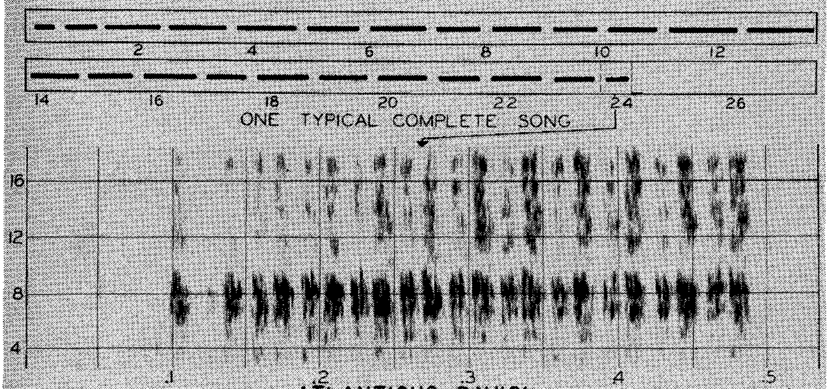
The rhythm patterns illustrated in Figures 9-11 are all reversible patterns—that is, they could be played backward and still have about the same structure, and probably about the same effect upon the insects which respond to them. However, in several subfamilies of Orthoptera and Cicadidae there have developed patterns of a "program-like" or irreversible nature, more like the bird song patterns discussed and illustrated elsewhere in this publication. Some of the patterns illustrated in Figure 12 are of this nature. Thus, the three-pulse phrase of *Amblycorypha oblongifolia* (De Geer) begins with a long-drawn-out pulse in which the toothstrike rate is gradually accelerated in a peculiar fashion. The phrases of *Conocephalus nemoralis* (Scudder), like those of most meadow grasshoppers, are composed of two parts, or two pulse rates, giving the effect of a series of ticks followed by a buzz. The song of *Orchelimum volantum* McNeill demonstrates still another kind of irreversible pattern, introducing a gradual change in pulse rate as each phrase is terminated.

An extreme in this tendency toward the development of more and more complex song patterns is exhibited by the male calling song of *Amblycorphla uhleri* Stal, illustrated in Figure 14. This song is probably the most complicated insect sound known in the world. It is composed of several different kinds of pulses, including some made by striking only one tooth of the stridulatory vein at a time. It has at least three different pulse rates, and it incorporates both gradual increases and gradual decreases in intensity. All of these characteristics are delivered in about the same way each time an individual sings, in a complicated sequence lasting up to a minute and a half and rarely less than 40 seconds. Variations in the length of the entire sequence are due to differences in the length of the various parts, rather than to the omission of particular parts of the song. The behavioral significance of different parts of the song represents a still unsolved problem. However, there are indications that this species and others in the genus, as also with the meadow grasshoppers (Conocephalinae), have isolated different functions of the calling song into separate and different rhythms which are produced in sequence in each repetition of the calling song. For example, in the meadow grasshopper songs which consist of a series of ticks followed by buzzes, the ticks are frequently left out at night, and when two males are in close proximity an unusually large number of ticks is produced, with the buzzes sometimes left out completely.

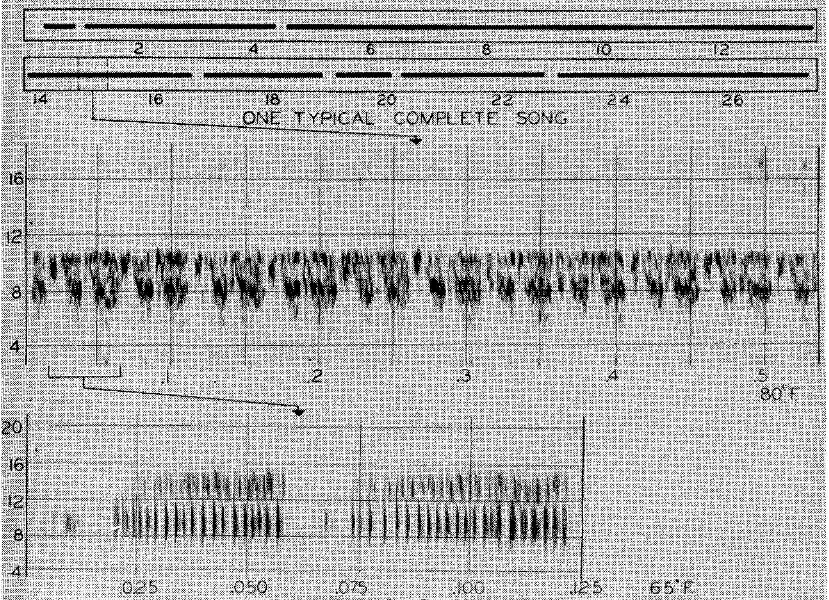
FIG. 11. The calling songs of three species of katydids (Decticinae), illustrating secondary groupings of pulses. Top to bottom: Pocohontas Co. W. Va., 11 Aug. 1955; Franklin Co. O., 27 July 1954; Franklin Co. O., 15 June 1954. (Ordinate, kc/sec.).



ATLANTICUS MONTICOLA



ATLANTICUS DAVISI



ATLANTICUS TESTACEOUS

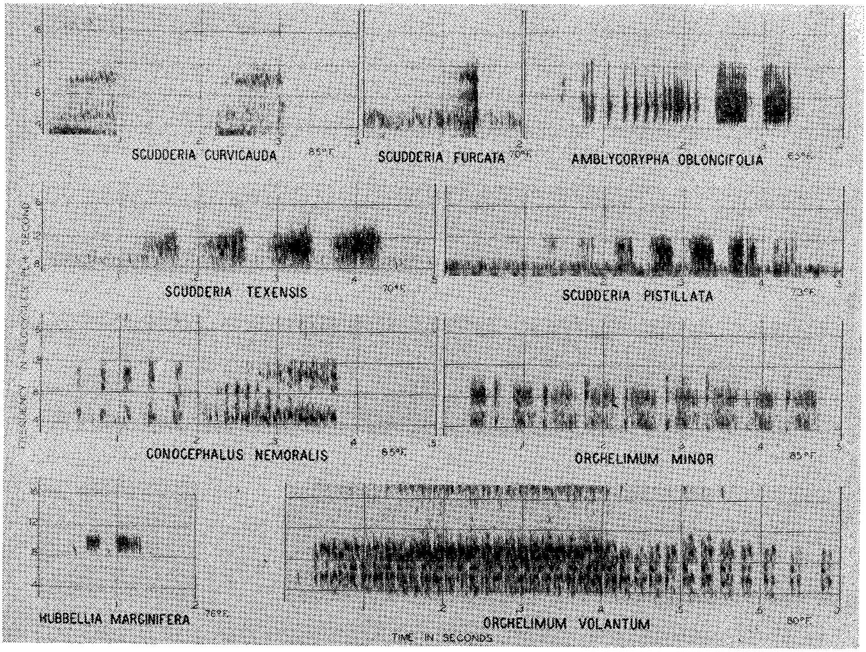


FIG. 12. Phrases from the calling songs of several species of Tettigoniidae, illustrating various degrees of complexity. Top to bottom: *(left)* Franklin Co. O., 8 Aug. 1954; Franklin Co. O., 23 Aug. 1954; Franklin Co. O., 17 Sept. 1954; Raleigh, N. C., 8 Aug. 1955; *(center)* DuPage Co. Ill., 18 Aug. 1954; *(right)* Carroll Co. O., 14 Aug. 1954; Champaign Co. O., 24 Aug. 1954; Hocking Co. O., 4 Sept. 1954; Pickaway Co. O., 26 Sept. 1954.

This would suggest that a visual stimulus is essential in the production of the ticks, as has also been suggested for the very similar song of *Magicicada cassinii* (Alexander and Moore, 1958). It is possible that the ticking part of the song of a meadow grasshopper is connected chiefly with the function of spacing of individual males and the buzzing represents the female-attracting part of the sound. In *M. cassinii,* both parts of the song are apparently essential to synchronization in chorusing which in turn is essential to success of the song chorus in attracting outside individuals.

Figure 15 shows the details of structure in the songs of ten species of cicadas. All of the *Tibicen* songs are illustrated by brief sections taken out of the middle of the songs, which in this genus are characterized by an initial swell in intensity accompanying the gradual introduction of the superimposed fluctuations in intensity (or disconnected pulse groups in some species) in the different songs, and then a corresponding de-

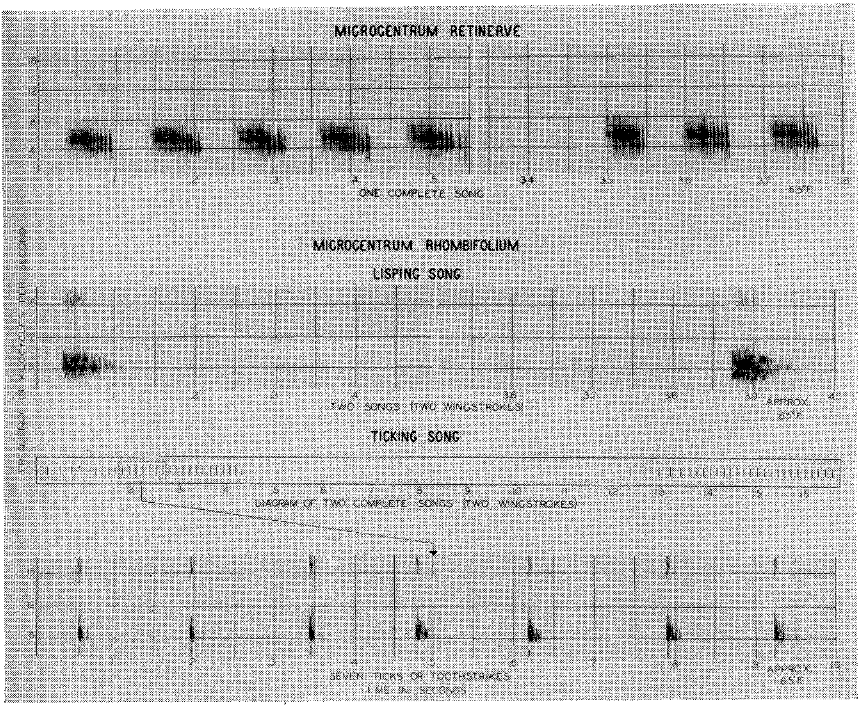


FIG. 13. The songs of two species of katydids (Phaneropterinae), showing the relationship of the lisping and ticking songs of *M. rhombifolium* to the calling song of *M. retinerve,* the only sympatric species in the same genus. Top to bottom: Pickaway Co. O., 10 Sept. 1954; Franklin Co. O., 21 Sept. 1954.

crease in intensity accompanied by the dying out of the superimposed rhythm elements as the sound terminates. The total song pattern in such species lasts from ten seconds to a minute or more, depending upon the species. In *Okanagana* and *Diceroprocta* species there is no such rise and fall in intensity, and the individual phrases, such as in the song of *O. rimosa* (Say), are repeated more or less continuously for long periods of time without change.

One of the most intriguing questions in the study of the evolution of song patterns, in insects as well as in amphibians and birds, is that of how differences in the song patterns of different species arise in the first place. It is not always necessary when new species develop for a completely new song pattern to appear. For example, in the genus *Nemobius,* there are several pairs of sibling species in which the male calling song of one species is almost identical to the male courtship song in the other species (Alexander, 1957c; Alexander and Thomas, 1959). Here, there

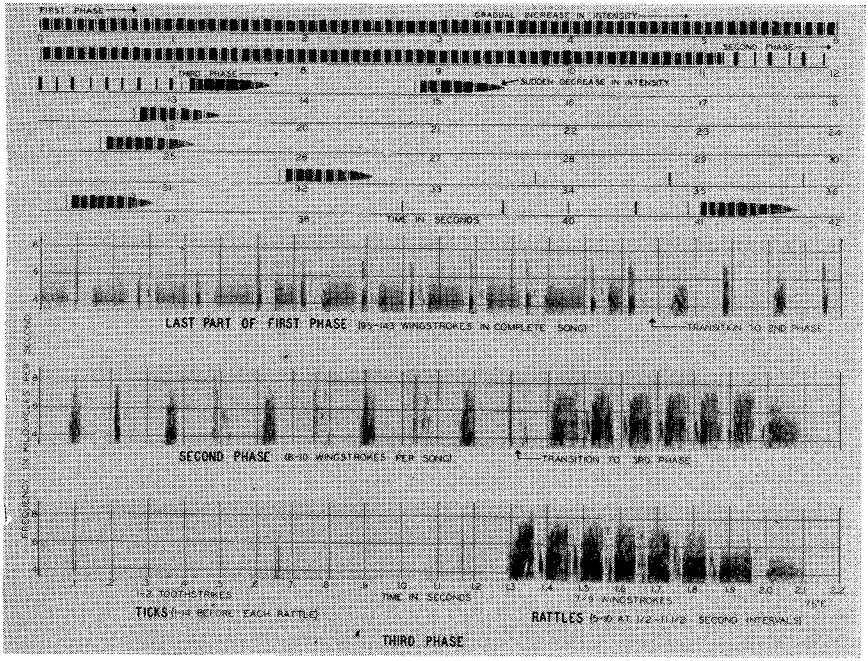


FIG. 14. The calling song of *Amblycorpha uhleri* Stal (Tettigoniidae: Phaneropterinae): diagram of a typical, complete song and spectrograms of portions of each phrase and each transition between phrases (Hocking Co. O., 3 Sept. 1954).

appears to have been just an alteration of the situation in which the male of one species produces a particular sound, and an alteration of the response of the females (and the males) to that particular sound. We may note that the male courtship sound is the only sound other than the calling song which is occasionally distinctive and repetitious enough, especially in crickets, to be involved in such a change in function. This phenomenon is probably not very common, and in most cases it appears that new song patterns have developed as species have multiplied.

It is important to remember that differences in rhythm pattern can arise in the calling songs of incipient species without any change in the external sound-producing apparatus. When differences in the sound-producing apparatus do appear in closely related species, they seem generally to be incidental to the significant song differences. For example, differences in pulse rate in simple trills in the Ensifera can arise in at least three different ways without requiring a change in the stridulatory apparatus: 1) a change in the actual speed of wing motion (distance moved per unit time), as in *Atlanticus testaceous* (Scudder) and *A.*

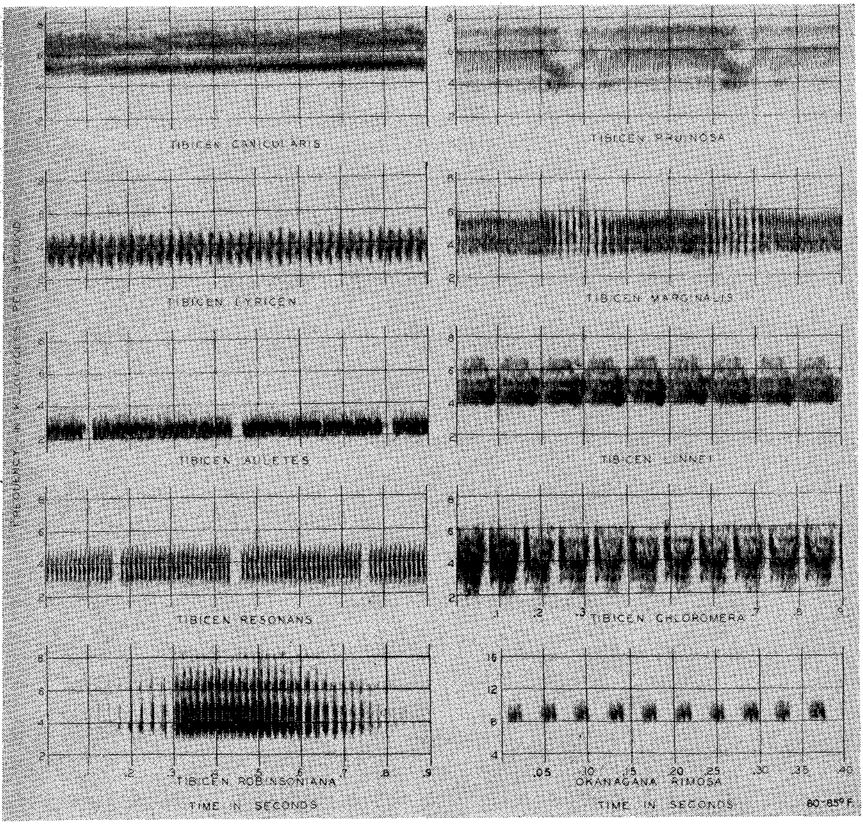


FIG. 15. Sections from the calling songs of ten species of cicadas. See text for explanation. Top to bottom: *(left)* DuPage Co. Ill., 26 Aug. 1954; Hocking Co. O., 4 Sept. 1955; Hocking Co. O., 12 July 1955; Harnett Co. N. C., 10 Aug. 1955; Adams Co. O., 9 July 1954; *(right)* Pickaway Co. O., 10 Sept. 1954; Lawrence Co. O., 4 Sept. 1955; DuPage Co. Ill. 20 Aug. 1954; Hocking Co. O., 4 Sept. 1954; Ashland Co. O., 26 July 1955.

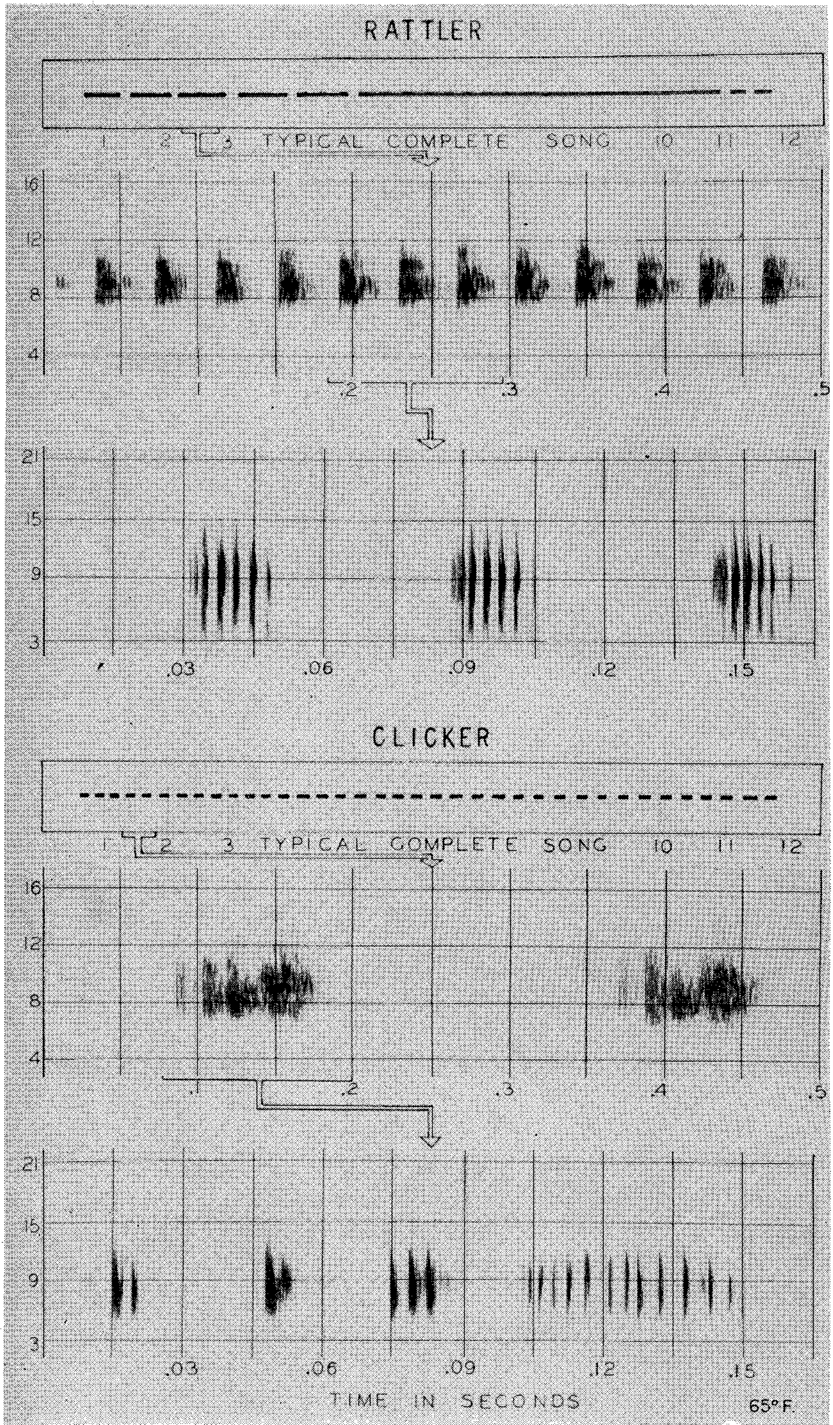
davisi Rehn and Hebard (Fig. 11), 2) a change in the length of the stroke of the wing without any particular change in the actual speed of its movement, as in *Nemobius carolinus* Scudder and *N. melodius* Thomas and Alexander (See Alexander, 1957c), and 3) the introduction of "wing hold" intervals of variable length between pulses as in *Nemobius tinnulus* Fulton and *N. allardi* Alexander and Thomas (Alexander and Thomas, 1959).

There is little evidence as to how the differences in song patterns of sibling species are inherited. Fulton (1933a) found that hybrids between *Nemobius tinnulus* and *N. allardi* (formerly considered erroneously under the name, *N. fasciatus* (De Geer)—cf. Alexander and Thomas, 1959) had pulse rates intermediate between those of the parent species, and that backcrosses moved the pulse rate of the F_2 generation partway toward that of the parent used in the backcross. Alexander (1957b) reported that a presumed hybrid between two chirping species of *Acheta* (*pennsylvanicus* (Burmeister) and *fultoni* Alexander) had the pulse rate of one parent, the chirp length of the other, and a chirp rate intermediate between the two. Perdeck (1957) found that hybrid males between *Chorthippus biguttulus* L. and *C. brunneus* Thunb. had song patterns with intermediate characteristics.

When one begins to compare the songs of sibling species in groups which possess highly complex songs, the problem of origin of differences becomes a great deal more puzzling. Figure 16 and Selection 5 compare the songs of two species of katydids which are both presently considered under the specific name, *Amblycorypha rotundifolia* (De Geer), and which will be referred to here as the "rattler" and the "clicker," respectively. These two species are thus far completely inseparable on a morphological basis. There is little doubt as to their distinctness. They have different geographic ranges, the clicker being a southern species ranging north in eastern United States into southern Ohio, and the rattler being a northern species extending southward to the southern border of the Appalachian Mountains. Their ranges overlap about 200 miles across the Appalachians, and their general distribution is very similar to that of other pairs of closely related species of Ensifera in eastern United States (Alexander, 1957b, and unpublished data; Alexander and Thomas, 1959). In the field the two species mature at the same time of year, sing at the same time in the evening, and in their overlap zone they frequently occur together in the same habitats, individually intermixed together in colonies. When placed next to each other in the laboratory in large cages, each containing about 25 males, the two species chorused independently of each other, indicating that each was unaffected by the singing of the other.

Figure 16 shows pen and ink diagrams of typical complete song patterns of these two species, then successive elaborations on spectrograms of parts of the patterns. In each case the pattern is complex and irreversible. The song of the rattler is composed of groups of similar pulses which become progressively longer, finally terminating with a single, long pulse group usually followed by one to three short pulse groups. All of the

FIG. 16. The calling songs of two sibling, sympatric species presently included under the name, *Amblycorypha rotundifolia* (De Geer) (Tettigoniidae: Phaneropterinae) (Hocking Co. O., Aug. and Sept. 1954). From Selection 5. (Ordinate, kc/sec.).


RATTLER
1 2 3 TYPICAL COMPLETE SONG 10 11 12
16
12
8
4
.1 .2 .3 .4 .5
21
15
9
3
.03 .06 .09 .12 .15
CLICKER
1 2 3 TYPICAL COMPLETE SONG 10 11 12
16
12
8
4
.1 .2 .3 .4 .5
21
15
9
3
.03 .06 .09 .12 .15
TIME IN SECONDS
65°F.

pulses in this song are alike, and each contains six to eight toothstrikes. In the clicker, on the other hand, the successive pulse groups in the song are of about the same length though there is a slight reduction in the rate at which they are produced as the song progresses. Each pulse group is in itself an irreversible pattern composed of three or four pulses, of which the last is much longer (contains more toothstrikes) than the first two or three.

To the human listener, these songs appear to bear no relationship to each other. However, a closer examination reveals that they have many similar structural characteristics. Each song is composed of groups of pulse groups, and the structure of the individual toothstrikes appears to be identical. Furthermore, the songs are about the same length, they are produced in chorus in the two species in the same way, and they are produced at intervals of similar length in the singing of lone males. The stridulatory apparatus in the two species appears to be identical. Since we know nothing of the behavioral significance of different parts of the sounds, it is useless to speculate concerning which of their differences are significant to the individuals of the two species. The origin and development of complex song differences in very closely related species such as these pose some interesting questions.

The only instance in which the song patterns of different species of insects are known to the writer to be identical is the case of three bush katydids in eastern United States, *Scudderia furcata* Bruner, *S. cuneata* Morse, and *S. fasciata* Beutenmuller. The males of these species all produce simple, one-pulse lisps (Fig. 12). However, they are in the group (Phaneropterinae) in which the females of many species produce answering sounds. It would be particularly interesting to investigate the timing of the responses of the females of these three species to the male's sound.

It has been suggested that because the calling songs of insects (and other animals) operate as they do, and because there has been such intense selection for specific distinctiveness, it follows that these sounds are poor indicators of phylogenetic relationships. However, it should be pointed out that even the simplest insect sound (for example) has more than one structural characteristic, and not every one of these will be of equal value to the animal in terms of behavioral significance. In most cases, the songs of sibling species of insects are widely divergent with respect to one or a few characteristics only, and when all structural features are taken into account one cannot escape placing the songs where they belong phylogenetically. Even in the extreme case in *Amblycorypha* cited above, and in the case of the seventeen-year cicadas in which the songs seem at first totally unrelated and sympatry is as nearly complete as it could be (Alexander and Moore, 1958), a careful analysis of the songs leads one inevitably to the conclusion that the species involved are closely related. When more than one kind of sound is produced by a species, a comparison of all the different sounds and the situations in which they are produced is the most reliable method of using this facet of the animal's behavior to help in determining relationships. Thus, Alexander (1957c) found that two species of *Nemobius* with calling songs that at first did not appear to be closely related had certain peculiarities of starting and stopping that suggested a close relationship, and this hypothesis was borne out by comparing the courtship sounds and later the specimens when the species responsible for the sounds were identified.

THE EVOLUTION OF SPECIALIZED CHORUSING BEHAVIOR

Along with the development of rhythmical units in the songs of individual insects, there have developed certain characteristic tendencies for the neighboring males in colonies to synchronize, alternate, or combine in some unusual fashion, the individual phrases or pulses of their songs. This results in an intensification of the total sound produced by the colony and in most cases causes a concomitant emphasizing of particular elements of rhythm which would otherwise be obscured in direct proportion to the number of individuals singing at once. Such specialized chorusing has obviously arisen many times, and similar forms of chorusing behavior have developed in insects with sound communication systems of separate origin, indicating a strong selective advantage and an origin in basic patterns of behavior common to most or all singing insects.

The simplest kind of chorusing behavior consists merely in the starting of song by a large number of individuals in a colony in response to hearing the starting of song by other individuals. This results in bursts of singing separated by nearly or entirely silent intervals. Such behavior probably occurs in most or all singing insects to some degree, and in eastern United States is most clearly exemplified in species of *Atlanticus, Amblycorypha, Neoconocephalus,* the flight-crepitating Oedipodinae, and the Cicadidae.

Synchronization of Song Phrases

This behavior occurs in one form or another in both Orthoptera and Cicadidae. Fulton (1928, 1934) demonstrated synchronization in *Oecanthus niveus,* and discussed it in several other species. Field observations and tape recordings in our laboratory verify that it occurs in the following species in eastern United States: *Oecanthus niveus* (De Geer) (Gryllidae: Oecanthinae); *Cyrtoxipha columbiana* Caudell, *C. gundlachi* Saussure (Gryllidae: Trigonidiinae); *Neoconocephalus nebrascensis* (Bruner), *N. caudellianus* (Davis), *N. exiliscanorus* (Davis), *Pyrgocorypha uncinata* (Harris) (Tettigoniidae: Copiphorinae); *Orchelimum vulgare* (Harris), *O. glaberrimum* (Burmeister) (Tettigoniidae: Conocephalinae). Faber (1953) lists several species of European Orthoptera which chorus in this fashion. Allard (1946) reported synchronized chorusing in *Magicicada cassinii,* and this was verified experimentally by Alexander and Moore (1958).

By listening to tapes played back at reduced speeds and by examining spectrograms it can be determined that in the crickets and katydids which synchronize, one individual starts his phrase just after the beginning of a phrase by the other individual with which he is synchronizing. Thus, one individual becomes a sort of leader, the other a follower. That the two individuals do not bear identical relationships to each other in this interplay is illustrated by the fact that silencing of the leader almost always causes the follower to stutter or stop, while silencing the follower rarely has an effect upon the leader.

An interesting similarity already mentioned occurs between the songs of *Orchelimum vulgare,* a meadow grasshopper, and *Magicicada cassinii,* a cicada. Both of these species have songs composed of a series of ticks followed by a buzz, or in other words, a slow pulse series followed by a rapid pulse series. Both species synchronize in chorus on sunny, still days in dense colonies, and in both cases the synchrony is largely a matter of synchronizing the two different parts of the songs. Thus, all the individuals tick together, then they all buzz together. A noteworthy difference is that in *cassinii,* short bursts of flight occur between buzzes and usually during part of the ticking, while *vulgare* does not fly during song, though it does sometimes walk or turn about while ticking. Alexander and Moore (1958) suggest that in *cassinii,* synchrony is probably a combination of the effects of visual and auditory stimuli, with the visual stimuli largely connected to the short flight bursts between buzzes. In *vulgare,* there seems to be a connection between ticking and visual stimulation, but synchrony can occur when the individuals are not within sight of each other and are not moving about at all.

In some meadow grasshoppers, a peculiar form of alternation sometimes occurs between neighboring males which are singing in very close proximity. In a quart jar containing two males of *Orchelimum agile* (De Geer) it was noticed in our laboratory that while the sound being produced was much like that produced by a single male singing alone, one male did all the buzzing while the other produced all the preliminary ticks. Two such groups of males were tape-recorded and observed on several different days, and each time this peculiar chorusing was maintained for long periods of time. The males were caged much closer together than is normal for singing males in the field. At particular times, different individuals were producing the different parts of the song, this perhaps depending upon which one started singing, or the relative positions of the two males in the cage.

Alexander and Moore (1958) reported a similar response under unusual conditions with *Magicicada cassinii*. A tape recording of the calling song of this species was played to males in nearby trees, which were not normally singing because of unfavorable weather conditions. When the first half of a phrase was played and then the sound was abruptly cut off, the males finished the phrase, but then dwindled off without chorusing through another phrase. When the second half of the song phrase was played, and the sound was abruptly stopped afterward, the insects chorused the first half of their normal song phrase and then dwindled off without finishing the phrase in chorus.

Alternation of Song Phrases

This behavior is well illustrated by *Pterophylla camellifolia* (Selection 4). An individual of this species singing alone delivers song phrases at a rate of four to six in five seconds at 80° F. However, when two individuals are singing near each other, each delivers phrases slightly more than half this fast, and the two alternate phrases so that about the same rhythm is produced by two males singing together in alternation as by a single male singing alone. When a large number of these katydids are close enough together while singing to react to each other, the result is a sort of synchronized alternation in which each male is in alternation with the neighbor he hears most clearly and also in synchrony with other males alternating with his neighbor. The result is a great, pulsing sound which fills the air for hours when there is no interrupting wind or rain. In eastern United States this kind of chorusing has been recorded only in the Appalachian Mountains where the woods are continuous for considerable distances and support tremendous populations of this species.

Alternation of song phrases occurs also in one form or another in many Acridinae, and in *Amblycorypha oblongifolia* (De Geer), *Orocharis saltator* (Uhler), *Microcentrum rhombifolium* (Saussure), and doubtless in many other species in at least a rudimentary form (Fulton, 1934). In some Oedipodinae there is a sort of chain reaction in flight crepitation in which one individual crepitates, his nearest neighbor follows immediately, a third individual or group of individuals follows the second, and a wave of sound and flight is thus generated, sometimes for a considerable distance and involving large numbers of individuals (Isely, 1936).

It is important to remember that in any species exhibiting at one time or another some degree of specialized chorusing, optimal chorusing may occur only under very special conditions, such as on clear, calm days (*Magicicada cassinii*) or on calm, warm nights (*Pterophylla camellifolia*), and only when large, dense colonies are involved. In some species, such as *Oecanthus niveus* and *Neoconocephalus nebrascensis*, it is unusual to hear individuals singing out of hearing range of all others, and thus synchrony can be detected almost every time one listens to singing individuals. On the other hand, singing males may be very close together, even in these species, and still not always sing in perfect synchrony. It is likely that whether or not two individuals in close proximity are synchronizing or alternating depends upon the intensity with which each insect hears his own sound as compared to the intensity with which he hears the sounds of other individuals. By means of a sound level meter, we have found that a tree cricket stridulating with his tegmina at a 90° angle produces the most intense sound almost directly behind him, while the auditory organs are located on the front tibiae. Thus, it would not be unusual for an insect to be in a position such that he could hear a neighbor more intensely than he could hear himself, and under such conditions he presumably would continually adjust the time of production of his own phrases according to his neighbor's singing rate rather than according to the rate at which he would sing if alone. It is clear that synchronization and alternation involve continual adjustment of each individual rhythm unit over long periods of time rather than simply the adjustment to a general rate of singing similar or identical in different individuals. If the intensities with which each of two individuals singing in close proximity is receiving his own sound and that of his neighbor are enough alike, or if each individual hears his own sound more strongly than that of his neighbor, then each may either alternately respond to his own song and to that of his neighbor, or fail to synchronize or alternate at all until the situation changes.

In eastern United States, all of the species exhibiting specialized chorusing live on vegetation, not one of the approximately 43 species which live on the ground synchronizing or alternating the calling song in chorus. Among the crickets, only night-singing species which live in trees or tall shrubs synchronize. Among the Tettigoniidae, all species which synchronize in chorus (except for the meadow grasshoppers and their special kind of synchronization) live either in trees or in bushes or tall weeds, and all are strictly night-singers. As mentioned earlier, certain correlations between habitat and time of singing are also evident (Fig. 2). All tree-inhabiting Ensifera in eastern United States are strictly night-singers, singing in the daylight hours only late in the season when the nights are consistently so cold that they cannot sing at their normal daily intervals. The correlation between habitat or height from the ground and time of singing is so consistent that within species groups there are differences in the time of singing associated with species differences in habitat. *Oecanthus pini* Beutenmuller lives in pine trees and it sings only at night. The other four or five species in the *Oecanthus nigricornis* group sing both day and night and live on weeds and grasses, usually less than four feet above the ground.

The significance of all these rather peculiar correlations between habitat and singing behavior is largely undemonstrated. There would seem to be a distinct advantage in loud, sedentary, chorusing species performing only at night, and thus being less susceptible to predation by birds. The relationship between song rhythm and habitat may be affected by whether or not the species can fly, and whether or not it does fly in connection with assembly through sound communication. There may be some significance in the fact that the sound of a calling male perched up on vegetation is carried more directly to other males and to females, even if the females are on the ground, than the sound of a male calling from dense ground cover when other males and females are also on the ground.

Busnel (1954), in dealing with 22 species of European Orthoptera, has correlated the production of simple, intense, continuous calling songs with low population densities and few acoustical obstacles in the species environment (e.g., vegetation-inhabiting Tettigoniidae), and the production of complex, soft, intermittent calling songs with high population densities and many acoustical obstacles in the species environment (e.g., ground-inhabiting Acridinae). These generalizations are far too simple to apply to the singing insects of eastern United States. For example, they do not take into account phylogenetic relationships, and Busnel's classification significantly places all the Acridinae in one group and all the Tettigoniidae in the other group. In the eastern United States one can take just the fifty-odd species of Tettigoniidae which live on herbaceous vegetation and find both simple and complex, soft, intermittent sounds (*Atlanticus, Scudderia, Amblycorypha* spp.), both soft and intense, simple, continuous sounds (*Conocephalus, Orchelimum, Neoconocephalus* spp.), both simple and complex, intense, intermittent sounds (*Scudderia, Microcentrum, Amblycorypha* spp.), and many other combinations of song types which, in addition, do not obviously correlate with variations in population density. Conversely, one can find a particular song type in all kinds of ecological locations, such as simple, intense, continuous trills in ground-inhabiting *Acheta* spp., herb-inhabiting Oecanthinae, and treetop-inhabiting Oecanthinae. When a large number of species and situations are considered, it is obvious that correlations between different types of song must take into account not only habitat and population density, but also phylogenetic relationships, present and past "sound environments," modes of assembly, susceptibility to predation, sedentariness of the singing males, and probably many more obscure factors. No simple comprehensive generalization appears possible at this stage in our knowledge.

The Origin of Specialized Chorusing Behavior

In terms of the production of song, an individual male can be regarded as composing two feedback circuits, one of them completely internal and the other partly external, involving feedback through the auditory organs. It is the influence of the external circuit upon particular units in the song patterns of males of different ages, different histories, and different species that is involved in the origin and evolution of specialized chorusing behavior. That the internal circuit can operate alone under certain circumstances is demonstrated by the production of the normal, rhythmical song in deafened individuals of *Oecanthus niveus* and *Acheta pennsylvanicus.* The significance of the external circuit, on the other hand, is demonstrated by all kinds of specialized chorusing behavior and also by the failure of deafened individuals of the above species to produce song uninterruptedly for as long periods of time as do non-deafened individuals.

Specialized chorusing has arisen whenever the males of a species have begun to respond to the phrases of their neighbors in a fashion similar to their responses to auditory feedback in their own songs. On the basis of the way that singing males respond to each other, chorusing insects can be divided into two groups: 1) those in which neighboring individuals merely stimulate each other into song (and perhaps keep each other singing over relatively long periods of time) without any interplay with respect to individual rhythm units in the song, and 2) those in which there is in addition a continual interplay between neighboring individuals (synchronization or alternation) with respect to the rate or rhythm of production of the individual phrases in their songs. The second group seems to include every species in which the normal calling song contains a precise or highly uniform chirp or phrase rate within the range of two to five per second; the first group probably includes all other singing species, or in other words, all species which have no precise rhythm unit within this range in the calling song.

Auditory feedback is a necessary coincident to the possession of auditory organs in sound-producing animals, even in cases such as that suggested for some cicadas by Pringle (1954) in which the auditory organs are rendered partially insensitive during sound production. It is also an appropriate mechanism for relieving a singing individual from the disturbing influence of other stimuli in the immedate surroundings, and as such its influence has apparently been elaborated in most singing insects in connection with selection for the ability to produce sound uninterruptedly for long periods of time. Auditory feedback can operate most efficiently in long-continued singing when successive rhythm units are delivered with a high degree of regularity. Constancy of rhythm pattern is also an important characteristic in rendering insect songs distinctive and recognizable to the members of the species. Thus, the independent appearance of similar forms of specialized chorusing behavior in different groups of singing insects seems based upon the re-inforcing interaction between 1) the development of regularity in the rate of production of phrases delivered within a range susceptible to successive stimulation through auditory feedback, and 2) an elaboration of the influence of external feedback. Whenever the sexual behavior and the particular song pattern of a species combine to make a chorusing colony a more efficient assembling mechanism than a non-chorusing colony, then the colony itself begins to operate as a feedback mechanism, continually enhancing by its own operation, its stability and its effectiveness as an attracting force. Under these conditions, it might be expected that relatively great alterations might occur in the assembling behavior and also in the song pattern and the conditions under which it is produced if these alterations increase the overall likelihood of optimal chorusing occurring. *Magicicada cassinii* perhaps represents an extreme in the elaboration of specialized chorusing behavior. There is evidence that in this species there is a great difference in the effectiveness of synchronized choruses as compared with non-synchronized choruses or partially synchronized choruses in assembling the males and females (Alexander and Moore, 1958).

The two most obvious ways in which specialized chorusing functions are by 1) emphasizing particular elements of rhythm which would otherwise be obscured in direct proportion to the number of individuals singing at once, and 2) intensifying the total sound produced by a colony, thus increasing the range of its effectiveness. However, if the interactions between individual males are comparable to successive induction—of antagonistic spinal reflexes in vertebrates (Sherrington, 1947) and of sequences of different kinds of complex activities in aphids (Kennedy, 1958)—then it is apparent that just as a single individual with efficient auditory feedback is a more stable sound-producing unit than a male lacking auditory feedback, a pair or group of chorusing males is a more stable sound-producing unit than a single male alone, not only because more individuals are involved, but also because of the successive induction of phrase production from individual to individual. Several observations on the responses of singing males of various species to artificial sounds and other unusual situations suggest that this analogy is a proper one.

Two mechanisms which appear to be operative in both synchronization and alternation can be described as 1) a stimulation to produce sound upon hearing a particular kind of phrase, and 2) an inhibition of sound production for a species-specific interval after hearing a particular kind of phrase. These two mechanisms are both demonstrated in the reactions of a male katydid, *Pterophylla camellifolia,* to a typewriter tapped in imitation of his song and as various kinds of deviations from it. A male of this species, normally a night-singer, was noticed to be singing consistently during the day when someone was typing in the neighboring room. To see if the typewriter was influencing the katydid, it was tapped in imitation, and the katydid slowed his rate of phrase production immediately in alternation with the typewriter taps. The katydid was then placed near the typewriter, and several hours of his reactions to various typewriter sounds were noted and recorded over a period of several days. The katydid could be stimulated into song at any time by the typewriter, even at times when he repeatedly stopped singing a few phrases after the typewriter had been discontinued. His rate of production of pulses within phrases could not be altered even by gross changes in the rate of pulse production in the typewriter phrases, but if the typewriter pulses were produced very slowly, he responded to each as if it were a complete phrase. When the typewriter was tapped continuously at a very rapid rate, he did not produce a phrase until after the typewriter stopped, and then his phrases were produced more rapidly than usual for a time. This fits with the suggestion of successive induction very well, as does the fact that two katydids singing in alternation usually produce phrases together at a combined rate slightly faster than either would if singing alone. A katydid sings sooner after being stimulated by a phrase produced by another katydid than he does after being stimulated by a phrase he himself has produced, and it can be seen that this is essential for alternation, for if this interval were of the normal length, the second katydid would not sing soon enough to inhibit the production of the second phrase by the first individual. Presumably, if the typewriter had been tapped continuously for a very long period of time, the katydid would not have sung at all afterward. Unfortunately, the significance of this was not clear to us at the time, and such a test was not performed.

The inhibitory effect of hearing a phrase which begins just before the affected individual would have begun a phrase himself in normal singing is further demonstrated by interactions between males of different species caged in close proximity. Fulton (1934) discussed this in describing the interaction between males of *Orchelimum militare* Rehn and Hebard and *O. bradleyi* Rehn and Hebard. A single caged male of *Neoconocephalus exiliscanorus* in our laboratory synchronized with loud buzzes produced by the mouth at both slightly slower and slightly faster rates than he was singing when alone. When the artificial noise ceased he reverted quickly to his original rate. Much like the *Pterophylla* male he could change his singing rate only slightly, then, if the stimulating sound was further altered, he would stutter irregularly a moment and stop, or revert to his original rate, the particular reaction apparently depending upon the intensity of the imitation. When continual noises lasting several seconds were produced near his cage, this male produced phrases during intervals of silence between them, and remained silent during the prolonged noise.

Observations such as the above lead one to wonder if there has not been, in the evolution of interaction sequences of communicative nature, selection in some cases toward signals of "optimal" length. If this were true we might expect, for example, that the number of ticks per series ordinarily produced in the song of *Microcentrum rhombifolium* (Fig. 13, Selection 3) results in a more intense and more effectively timed response in the female than much shorter or longer series. Perdeck (1957) found that the rate of alternation of males with males versus males with females in *Chorthippus* species differs, providing a means of sex recognition.

THE ONTOGENY OF INSECT SONGS

Nearly all of the sound-producing insects, even those with complex calling songs such as *Amblycorypha uhleri,* overwinter in the egg stage and have no contact between individuals of any age from one generation to the next. Under such conditions, the faithful transmission from generation to generation of song patterns as complex as some of those described in this paper is quite a remarkable phenomenon. An individual in such species must be able to reproduce the calling song of his species without ever having heard any part of it produced by any individual other than himself. In species with simpler songs, as already pointed out, an individual can produce the normal calling song without having heard even himself. Walker (1957) has shown that virgin female tree crickets (Oecanthinae) orient and move toward the songs of their own males without having previously heard the sound and without previous contact with the males, and Haskell (1958) has demonstrated that subjecting young females of *Chorthippus parallelus* (Zett.) to various sounds during the last nymphal instars failed to change their response to the calling song of males of their own species or to make them responsive to any other sound.

There is little information available as to how the song patterns of insects develop in the individual. It is probable that the song is never produced perfectly and completely the first time the sound-producing apparatus is moved. A male field cricket in our laboratory was reared in isolation and then placed with a receptive female and another male which had already copulated several times. The courtship song in field crickets, as already discussed, is quite different from the calling song and involves a different position and kind of motion of the tegmina. Although both males immediately showed interest in the female, the previously isolated and unmated male obviously had some difficulty in developing the correct rhythm of vibration of the tegmina. After several seconds of starts and stops and almost soundless shuffling of the tegmina, the correct motion seemed to appear rather suddenly, and he began to actively court the female, which in this case had already entered into copulation with the other male. A similar case was discussed above in connection with the effects of the courtship song upon females in field crickets.

Kramer (1958) suggests that the initial imperfection in the singing of male crickets may be associated with the development of pigmentation in the wing muscles, but this does not seem likely since male field crickets do not begin chirping movements of the tegmina, even in aggressive contacts, until about three days after maturing, and Kramer points out that in cockroaches the pigmentation of the wing muscles develops during the first 72 hours after the molt to adulthood. Furthermore, imperfect chirping occurs temporarily in crickets which have been adult two weeks or more if they have not chirped previously.

Although most rhythm elements in insect sounds appear to be relatively inflexible, certain species have units in their songs which are at least temporarily modifiable to some degree. Thus, the phenomena of synchronization and alternation require temporary modifications in an individual's song pattern. Pierce (1948) reported that he was able to change the number of pulses per phrase emitted by a caged male of *Pterophylla camellifolia* after he had gotten the animal to respond to artificial stimulation of its sounds, simply by changing the number of pulses in the stimulating sound. It is well-known that in this species there is a considerable amount of variation in the number of pulses per phrase in the songs of individuals located in different colonies. It is also noticeable that the individuals in any given, dense colony are likely to be producing the same number of pulses per phrase, especially late in the night when they have been chorusing together for some time, and when the climatic conditions are conducive to perfection in chorusing. In our laboratory, the caged *Pterophylla* responding to the typewriter produced only two-pulse phrases, after producing a few one-pulse phrases when first starting to sing, as is usual in this species. However, when we stimulated him into song with three-pulse typewriter phrases, we were able to get him to sing three-pulse phrases consistently in alternation with the typewriter. After he had started alternating, it was usually difficult to change him from a two-pulse phrase to any other kind of phrase, but this could be done most easily by interspersing the typewriter phrases in such a way as to interfere with the rhythm of alternation, and by continuing to produce three-pulse phrases with the typewriter as this was done. Once he had changed to three-pulse phrases, he usually kept this kind of song going until two-pulse phrases were produced with the typewriter, which generally caused him to change immediately back to two-pulse phrases. Occasionally we were able to change him back and forth from one- to two-pulse phrases and from two- to three-pulse phrases, and vice versa, tapping out only one kind of each phrase at a time. This showed that he was responding to each individual phrase as it was produced. On one day we successfully altered his singing so that for a short time he consistently produced four-pulse phrases. We were never able to induce five-pulse phrases. There was some indication that it was easier to alter this male's singing after he had been subjected to phrases with unusual numbers of pulses over a period of several days, but this remains to be checked more carefully.

These experiments raise some interesting questions. For example, is the number of pulses per phrase sung by a lone male determined in part by sounds he hears early in his adult life, or is this genetically determined? The fact that even an old male's phrase length can be temporarily altered in spite of his continual tendency to slip back into a two-pulse phrase and to sing a two-pulse phrase when alone suggests that environmental influences may have been involved in the establishment of his normal phrase length. This species has two populations, northern and southern, respectively, which meet and apparently interbreed across a narrow zone in the Appalachian Mountains. The southern population produces three- to seven-pulse phrases, most often four- to six-pulse phrases. The northern population produces one- to five-pulse phrases, most often two- to three-pulse phrases. There is also a difference in the pulse rate within phrases. In the area in which these forms appear to intergrade, the pulse number per phrase is more variable than anywhere else in the range, with seven-, eight-, and nine-pulse phrases common, and occasional individuals producing pulses continually in series of 25 to 30 without pausing. Whether this particular erratic behavior is due entirely to the genetic make-up of the hybrids or is largely a product of the behavioral interactions among the genetically different individuals maturing in this area remains to be discovered. Here again we may wonder what effect repetitions of song involving auditory feedback may have on the influence of the internal circuit. Is there a difference in the relative influence of these two circuits in the singing of individuals subjected to different noises early in their adult lives? For example, deafened males of the snowy tree cricket, *Oecanthus niveus,* sing normally but less if they are deafened after singing for some time, but several males deafened as nymphs never sang in our laboratory after maturing.

SOME GENERAL COMPARISONS

Apparently, only the vertebrates and the arthropods have evolved systems of sound communication. The arthropods were probably the first animals to utilize sound as a communicative mechanism—certainly the first to utilize it as an air-borne signal. The rudiments of modern orthopteroid sound communication can be traced to behavior patterns occurring in the Paleozoic orthopteroid ancestor, and the antiquity of arthropods and the extent of specialized sound production in modern species suggests that it probably originated much earlier.

Sound communication has arisen independently hundreds of times in the arthropods and today occurs in tens of thousands of species—far more than in all other kinds of animals combined. There is evidence for special sound-producing apparatus and special auditory organs in hundreds of families of insects involving nearly every pterygote order.

The most complex arthropod sound signals involve fewer dimensions than the more complex vertebrate signals (for example, rhythmic fluctuations in frequency—melodies—are lacking), but within the dimensions utilized, a high degree of intricacy and efficiency is realized. The auditory sense is probably exceeded in the complexity and multiplicity of its functions as an intraspecific communicative device in arthropods only by combinations of tactile apparatus, and by the visual sense in connection with rhythmic "dances."

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CAPTIONS TO SELECTIONS ON DEMONSTRATION RECORD

Selection 1. The repertoire of a male field cricket, *Acheta pennsylvanicus* (Burmeister) (Gryllidae: Gryllinae), played at normal speed, then at one-fourth speed (Franklin Co. O., June, 1954).

Selection 2. The repertoires of the males of the seventeen-year cicadas, *Magicicada septendecim* (Linnaeus) and *M. cassinii* (Fisher) (Homoptera: Cicadidae) (Brood XIII, DuPage Co. Ill., June 1956).

Selection 3. The repertoires of the male and the female of the katydid, *Microcentrum rhombifolium* (Saussure) (Tettigoniidae: Phaneropterinae) (Ann Arbor, Michigan, August, 1958).

Selection 4. The repertoires of the male and the female of the katydid, *Pterophylla camellifolia* (Fabricius) (Tettigoniidae: Pseudophyllinae) (Franklin Co. O., August 1954; Raleigh, N. C., August 1955; Pocohontas Co. W. Va., August 1955 (3); Ann Arbor, Michigan, August 1958).

Selection 5. The calling songs of two sympatric katydids presently recognized under the specific name, *Amblycorypha rotundifolia* (De Geer) (Tettigoniidae: Phaneropterinae), played at normal speed, then at one-fourth speed. (Hocking Co. O., August and September, 1954).