ARTHROPODS

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Four aspects of the communication systems of animals have received wide attention and seem most likely to yield generalizations of broad interest in biology: (1) general life functions served by the signals, (2) relationship of signal differences to speciation, (3) hereditary and environmental influences on signals and responses, and (4) neurophysiological mechanisms. In this review I shall concentrate on the evidence regarding these four topics. My coverage will be restricted to a comparison of five groups of arthropods: (1) crickets (Orthoptera: Gryllidae), (2) katydids (Orthoptera: Tettigoniidae), (3) grasshoppers (Orthoptera: Acrididae), (4) cicadas (Homoptera: Cicadidae), and (5) fireflies (Coleoptera: Lampyridae). Further, I shall compare only the most prominent and elaborate communication systems of each group: acoustic in crickets and katydids, acoustic and visual in grasshoppers and cicadas, and visual in fireflies. Each of these systems includes a variety of signal patterns, and all of them have been studied extensively during the past decade. Indeed, with the exception of honeybee communication, and perhaps *Drosophila* courtship, no invertebrate communication systems have been analyzed as extensively as the acoustic and visual systems of these five groups of arthropods.

NATURAL SELECTION AND THE COMMUNICATION FUNCTION

Williams (1966) has rightly underscored an urgency that biologists stop shunting aside the necessity for serious, painstaking analysis of the precise adaptive significance of the attributes of living organisms that they are studying. We have dallied far too long with a casual attitude in this regard, leaving the problems to a noncumulative, anecdotal natural history and tolerating, in various biological subdisciplines striving to be quantitative, an almost complete divorcement from any concern over the selective value of characters being studied.

One of Williams' examples can be enlarged to demonstrate how silly is this approach to biology: It is the potential significance of insight into the unanswered question of how and why man's ancestor, among all primates, "suddenly" began a dramatic trend toward increase in brain size. Should we derive significant insight into this problem— precisely what were the selective forces, when in the lifetimes of individuals were they most powerfully effective, and how did they function through the social groupings of evolving man—can any doubt exist that essentially every endeavor of modern man would be significantly redirected?

The impact of this argument is more dramatic when it is applied to humans—partly because, in one way or another, all of us are more interested in humans than in other animals and partly because the details of human existence are so far removed from the selective contexts which shaped men that many of us would like to pretend there was never any important selection anyhow. But a lesson is here for all of biology. There are biologists as well as social scientists who argue by analogy and insist that one can analyze the mechanisms of, say, an automobile quite satisfactorily without the slightest notion of its purposes—of highways, drivers, passengers, climates, collisions, or any other such issues. But this is an empty and fallacious argument, for it requires that knowledge of the functional aspects of automobiles —versus total ignorance about them—would neither alter one's interpretation of their mechanisms nor accelerate his insight into them. The fact is that we are not free, as many biological writers have been telling us we are, to investigate *either* function *or* mechanism—we may be more intrigued by the complexity of one or the other in this case or that, but we are bound always to study both and to study them together. In this chapter I have tried to review briefly our knowledge of the functional significance of the five communication systems under consideration, already treated in detail in various recent reviews, and then to compare the systems with regard to the probable evolutionary interaction of changes in function and mechanism.

GENERAL LIFE FUNCTIONS OF SIGNALS

In a recent review (Alexander, 1967), I arranged the acoustic signals of arthropods under nine functional headings. Deleting food and nest site directives, which are limited to social species, and adding the function of aggressive mimicry recently reported in fireflies (Lloyd, 1965), nine known categories of signals can be listed, as follows, for the five communication systems discussed in the present review:

1. Disturbance and alarm (predator-repelling and conspecific-alarming) signals

2. Calling (pair-forming and aggregating) signals

3. Aggressive (rival-separating and dominance-establishing) signals

4. Courtship (insemination-timing and insemination-facilitating) signals

5. Courtship interruption (pair-reforming?) signals

6. Copulatory (insemination-facilitating and pair-maintaining) signals

7. Postcopulatory or intercopulatory (pair-maintaining) signals

8. Recognition (pair- and family-maintaining) signals (limited to subsocial and social species)

9. Aggressive mimicry (prey attraction by production of pair-forming signals of prey species)

Evidence for existence of these functions in the acoustic signals of arthropods has been reviewed in detail by Alexander (1967). Lloyd (1966), has published a similar review for fireflies, and Shaw (1966) and Spooner (in press) provide additional information concerning various katydids.

In this review I shall concentrate on the pair-forming function, as these signals are the most prominent, diverse, and species-specific and there is more opportunity to compare similarities and differences in signal-coding among species.

ARTHROPOD GROUPS INVOLVED AND
THEIR PAIR-FORMING SYSTEMS

Crickets and Katydids

Crickets and katydids comprise two families of insects, Gryllidae and Tettigoniidae, belonging to the order Orthoptera. They possess a common acoustic system in which the signaling device is a stridulatory apparatus on the forewings of the male and the auditory organs are tympana located within slits on the forelegs. These two devices have evolved together since at least Jurassic and were evidently present in the common ancestor of these two families (Alexander, 1962, 1966). Most crickets and katydids are nocturnal and employ vision only to a minimal degree in intraspecific communication; a few crickets and some groups of katydids (most notably those in the subfamily Conocephalinae, sometimes referred to as meadow grasshoppers) are more or less diurnal and possess acute vision.

Crickets and katydids have long antennae which bear both tactual–mechanical and chemical end organs. All crickets have in addition a pair of long, tactual cerci (or "rear-end antennae") which are re-

sponsive both to tactual stimuli and to intense airborne vibrations of relatively low frequencies. No evidence is available concerning whether or not the cerci are also sensitive to specific chemical stimuli, though this seems likely in view of the nature of the courtship behavior of crickets.

Although crickets and katydids have the same kind of acoustic system, they have evolved separately for such a long time that many aspects of their signaling system, such as the details of signal structure and function, can be compared almost as if entirely separate systems were involved. In most groups, only the males signal acoustically, and in all crickets and most katydids pair formation is effected by the females simply moving to the more or less stationary calling males. Many crickets, particularly Gryllinae and Nemobiinae (field, house, and ground crickets), have distinctive aggressive, courtship, and post-copulatory sounds in addition to the male calling sound. Female katydids in the subfamily Phaneroptinae make specialized noises functional during pair formation. Spooner (in press) describes three methods of pair formation in this subfamily: (1) the male makes a particular sound, the female answers with a tick, and the male goes all the way to the female; (2) the male makes one kind of noise which attracts the female from a distance (but not at close range), the male then makes a second noise which the female answers with a tick, and the male goes to the female from close range; and (3) the male makes one kind of noise, the female answers with a tick, the male moves toward the female from a distance (but not all the way), and the male produces a second kind of noise which attracts the female the remaining distance to the male. Some of these interactions involve intensity fluctuations in the male's sounds and specific responses to intensity changes. Sometimes males make sounds causing different responses in sequence, always together, and reponses to the different parts of the sequence occur at the proper times during the coming together.

It would seem that female signals are involved whenever the males have become the active locomotors during pair formation. Phaneropterine katydids and fireflies are two examples, with the situation most likely primitive in fireflies (Lloyd, 1966), but derived in Phaneropterinae from the situation more commonly found in Tettigoriidae and Gryllidae.

Grasshoppers

Grasshoppers also belong to the order Orthoptera and share the jumping hind legs of crickets and katydids, from the ancestor of which

they diverged most likely in late Paleozoic. Grasshoppers have relatively short antennae and are mostly diurnal, in contrast to the principally nocturnal crickets and katydids; their compound eyes are correspondingly large, and their utilization of visual signals is an impressive aspect of their sexual behavior. Color, size, shape, and motion, the last involving both the whole body and particularly the large hind legs, all seem important in close-range interactions.

Grasshoppers have evolved an acoustic system entirely separate from that of crickets and katydids. The auditory organs are tympana located at the base of the abdomen, and there are various kinds of stridulatory devices, the most common being the rubbing of the specialized hind legs against the wings or the abdomen. A notable addition, however, is the production of sound during specialized flight by males, principally in the subfamily Oedipodinae. The hind wings are opened and closed, producing a snapping or crackling effect usually referred to as crepitation. Crepitating flights are in many species associated with the exposure of pink, yellow, blue, or black-patterned underwings.

Though nearly all grasshoppers possess abdominal auditory tympana, curiously, a great many species do not crepitate or stridulate. Pair formation generally occurs in one of two ways; (1) the male is attracted to the female by her movement (silent species) or (2) the female is attracted to the crepitating or stridulating male, and the male is then attracted by her movement at close range. Males of some crepitating species seem to aggregate, probably as a result of hearing or seeing other males; whether these aggregations are in any way analogous to those found in other insects, such as cicadas, remains to be discovered.

After seeing a female, the male approaches and mounts her. In some species the male stridulates just before he begins this approach or during it—and some of these are cases in which males do not attract females from a distance by stridulation. In some species there is an exchange of stridulatory sounds between the male and female during pair formation. Some male grasshoppers also stridulate if disturbed during copulation or when other males are encountered (aggression?) (Jacobs, 1953; Haskell, 1957; Faber, 1953; Otte, personal communication).

Cicadas

Cicadas are insects in the order Homoptera. Unlike crickets, katydids, and grasshoppers, juvenile cicadas do not resemble the adults and do not live in the same habitats. Instead, they are subterranean,

subsisting on root juices and requiring several years to mature. Like the adults of most crickets, katydids, and grasshoppers, adult cicadas are short-lived, their populations usually lasting only a few weeks.

Most cicadas are strictly diurnal, and vision is very important in their close-range interactions. Chemicals may be less important to cicadas than to any of the other groups involved here, though, curiously, no one yet knows the precise stimulus responsible for the male initiating courtship or the female accepting him.

The acoustic system of cicadas is shared only by other members of the suborder Auchenorrhyncha—leafhoppers, treehoppers, spittlebugs and some other, similar, small sucking insects. Specialized, convex portions of the abdominal body wall (tymbals) are crinkled at rapid rates by a large pair of muscles probably derived from abdominal muscles. The auditory organs are tympanal structures located near the tymbals.

Some cicadas produce specialized sounds that are evidently communicative by clacking the wings together. Only male cicadas have functional tymbals, but wing-clacking is also known in females (Moore, personal communication). Presumably, many cicada signals function in the simple fashion of cricket calls, the stationary calling male attracting sexually responsive females. In numerous species, however, tremendous, dense aggregations of males are formed, within which the individual males keep up a continual alternation of song bursts and short flights. Functions of the different acoustic signals and the manner of pair formation and courtship have been carefully studied only in the genus *Magicicada* (Alexander and Moore, 1958, 1962, unpublished). In these species, which require thirteen or seventeen years to mature, the calling (or "congregating") songs of the males attract both males and females (Alexander and Moore, 1958), though visual stimuli are probably involved in the behavior of chorusing males at close range. It is extremely difficult to figure out what is happening in a cicada chorus, because so many individuals are involved, they are moving so rapidly and continually, and they are usually so high in trees that direct observation is difficult. In 1963, however, Dr. Thomas E. Moore and I spent several days in an area where only small isolated trees were left for the performance of a large population of emerging cicadas. I will describe our observations in some detail, as they represent a new method of pair formation among the groups discussed here, the first method known certainly in cicadas, and an explanation of the role of male phonoresponses and aggregations in pair formation.

On this occasion, our sixth year studying these cicadas in the field,

we decided (in desperation) to watch individual cicadas, describe the behavior we saw on tape more or less continually, and mark the cicadas we watched by snipping portions of their wings or legs according to a code that informed us whether that individual had been seen courting, copulating, performing in chorus, sitting motionless during chorusing, or ovipositing. Several days were required before significant numbers of repeats began to accumulate. Eventually, however, we repeated enough observations on marked cicadas to indicate, for example, that females mate several times and that a few hundred transported and released males and females of thirteen-year species (*tredecassini* and *tredecim*) mated freely with their respective siblings in the 17-year population we were studying (*cassini* and *septendecim*), but evidently never with any other seventeen-year species. Most importantly, we learned how pair formation is effected in the tremendous, active aggregations of these species. Females of a chorusing species fly into the active chorus, evidently attracted by the sound at long range, possibly by both sight and sound at close range. There they land and crawl out on a twig or leaf near the perimeter of the foliage on which the males are performing their game of "musical chairs." Once in this position, a female simply perches, motionless. The only other cicadas perched this way in chorus trees are ovipositing females, females that are for other reasons not sexually responsive, and generally relatively small numbers of individuals of the other two *Magicicada* species, which perform maximally at different times of the day and rarely in large numbers in the same trees. The chorusing male takes the initiative from here. If such a male happens to land within a few inches of a motionless cicada of any sex or species, he drops out of the chorus by failing to fly or sing again. Instead, he remains motionless, either where he landed or after walking or sidling close to the motionless cicada until he is nearly touching it. There are several characteristic positions for such pairs, but the previously chorusing individual generally faces the previously motionless individual.

A pair of cicadas thus formed may remain without further action for several hours. Unless disturbed, the pair breaks up either because one or the other individual flies away for unknown reasons without further contact or because the male eventually approaches close, begins courtship or begins to mount the approached cicada, and is either dislodged himself or causes the other cicada to fly away. Otherwise, the approaching male eventually begins courtship and the pair copulates, a process which sometimes lasts several hours. Once we had made this discovery, it became annoyingly obvious to us that nearly all of the nonperforming cicadas in a chorusing tree are paired off;

there may be thousands of noncopulating, noncourting cicadas simply sitting motionless in pairs, a fraction of an inch from one another, in such a tree.

We have no inkling of the stimuli determining whether a male eventually courts the individual he lands near, or simply rejoins the chorus, or what stimuli cause sexually responsive females to recognize the courtship of their own males. Males often court other males and begin mounting them, sometimes pursuing them tenaciously as they run along a branch. In one case we recorded that a pair of cicadas sat motionless facing one another with their antennae a fraction of an inch apart for three hours and then copulated. In other cases pairs broke up swiftly, or courting and copulation followed the landing of the chorusing male by only a few minutes.

During these observations we made two other important discoveries **that significantly altered our thoughts about periodical cicada behavior.** Contrary to our earlier beliefs, male cicadas almost always,
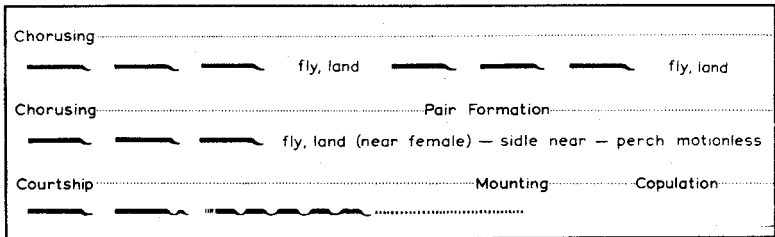
septendecim & tredecim
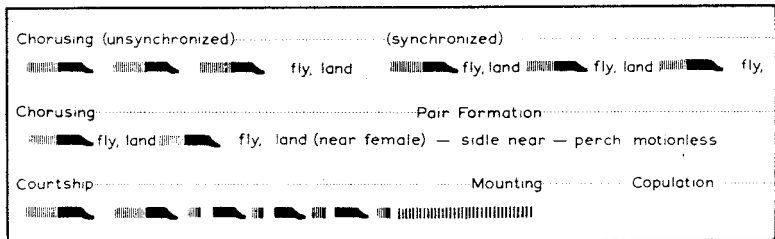
cassini & tredecassini

Approximate Time in Seconds (75°)

FIG. 1. Sequence (patterned after audiospectrographs) in which the three acoustic signals of two pairs of periodical cicadas are produced during sexual behavior. The third species pair, *Septendecula* and *tredecula*, behave similarly, but behavior during the first courtship sound has not been watched and no good tape recording has been made. Chorusing calls in these two species normally vary in length between about 1.2 and 3.0 sec.

perhaps always, produce acoustic signals during courtship—that is, when the male in a pair finally begins to approach and start copulation with the female. Further, supporting a tentative earlier observation by Alexander, we found that two distinctive courtship sounds are produced by all three species, always in a given sequence (Fig. 1). First the male produces a few phrases evidently identical with those in the congregating sound. Then he changes rather quickly to a sound that resembles congregating phrases run together. This sound is usually produced for only a few seconds, and the male switches immediately to a series of short, simple buzzes or pairs of buzzes just before and during his attempts to mount and engage the genitalia. This last sound may go on for several minutes. These sounds may be important signals to the female, but it seems likely that chemical and visual stimuli are also involved. Not surprisingly, the courtship signals of these cicadas, which mass together in three-species populations in most parts of their ranges, are specific and complex.

Fireflies

Fireflies are beetles in the family Lampyridae. Their most impressive communicative signals are produced by flashing or glowing mechanisms located in the abdomens of both the male and the female. For the most part, juvenile (larval) fireflies are even more unlike the adults than are juvenile cicadas. Some adult fireflies, however, resemble the larvae rather closely, and larvae and adults of fireflies actually live in more similar habitats than do the juveniles and adults of cicadas.

Fireflies are chiefly nocturnal; chemicals are probably of great importance at close range. Unlike any of the groups discussed earlier, the principal signaling device of fireflies is present in the larvae as well as the adults. The flashing and glowing signals of fireflies are not known to be produced other than during pair formation or disturbance, except that some larvae and adults glow continuously. Lloyd (1966, pp. 11–12) describes the flash communication of *Photinus* fireflies as follows:

> At the time of evening characteristic for the species, males arise from the grass and fly and flash, most of them keeping within an ecologically well-defined area such as a lawn, forest edge, stream bed, or wet corner of a pasture. Male flight paths during moments of light emission are characteristic for the species; some species can be identified by this behavior alone. . . . Females are found on the ground and on grass stems or other low vegetation. When a male receives a flashed answer from a female after a species-characteristic interval following his own flash, he turns and flies toward her. After a few seconds he repeats his flash-pattern; if he again receives the correct

flash response he continues his approach. Flight terminates a few centimeters from the female after from one to ten flash exchanges. After landing, the male usually completes the approach by walking and exchanging flashes with the female. Males mount females immediately upon contact. For complete attraction, only flash signals are necessary, and in all species tested, males were attracted to females caged in airtight glass containers. During approaches, females frequently fail to answer some of the male flashes, but when they resume answering, males continue their approaches. Males remain in the area of a previous response, emitting their flash-pattern for several minutes after females are removed.

In most species, activity lasts for about one-half hour and then decreases slowly over the next 30–40 minutes, until eventually only an occasional flash can be seen.

Lloyd's (1965a) discovery that predacious *Photuris* females give responses like those of females of *Photinus* prey species, and thus attract and eat *Photinus* males, is apparently unique. One of the intriguing questions raised is how *Photinus* has adjusted to this jeopardy—a topic that ought to interest pest control biologists currently enthusiastic about using sex signals as lures. But the questions of how many different *Photinus* species can be lured by one *Photuris* female and how the *Photuris* female's response develops and relates to her own sexual responses to *Photuris* males are even more intriguing. The neurophysiological possibilities are reminiscent of Spooner's discovery (in press) that some male katydids go to females that are answering other males. The female's soft ticks are meaningless alone or if improperly timed with the male's sound, but, to be attracted, a male need not be the one that made the sound the female is answering. In this case, calling males evidently have made two adjustments: (1) they soften their sounds as they approach the female, probably reducing the number of other males attracted by the exchange and (2) they deliver ticks resembling those of the female instantly upon completion of her response, which could lure "parasitic" males the wrong way. Possible significance relative to the neurophysiological basis for this behavior is found in Spooner's discovery that among species with two-part male calling sounds only one male in a group usually produces the first part of the song, the others chiming in as part two and another individual taking over part one if the original "leader" is silenced.

CODING OF PAIR-FORMING SIGNALS

As many as fifty species of insects which have acoustic signaling systems and fifteen species of fireflies may live together in the same

habitat in parts of eastern North America. Most are mature and perform sexually in middle or late summer; a few mature in spring and early summer, overlapping little with the later species. Differences in diurnal cycles separate some species; for example, the grasshoppers and cicadas are all active in the daytime, the crickets principally at night. Of course all fireflies are active during darkness, but some perform only at dusk, others only later in the evening. Habitat differences further separate many species during sexual performances.

Some of the seasonal, daily, ecological, and geographic differences among species signaling in the same sensory modalities are a result of selective action resulting from reproductive interference; in other cases the differences are effective in this context, though historically they may be incidental to it.

The actual pair-forming signals of species sexually active in the same places at the same times are always structurally different. Sometimes these differences too must have appeared without direct selective action caused by reproductive interference. A probable example is the frequency (hertz) difference between the calls of field crickets (Gryllinae) and ground crikets (Nemobiinae), which presently seem to reflect only that ground crickets are about half as big as field crickets. But the universality of signal distinctiveness when species live together, as well as identity or near-identity in the signals of some similar species that evidently have never lived together (Alexander, 1962, 1967), indicates that many differences have resulted from direct selective action. We may suppose that whenever two species that cannot amalgamate (because they produce inferior hybrids or are intersterile) come together geographically and ecologically, if their sex signals are not so different that little or no confusion ensues, then some adjustment will occur, either in signal structure or in the times and places of sexual activity. Sometimes courtship signals will be affected by such selection, and indirect effects often change aggressive and other signals as well. But the pair-forming signals are an appropriate focus, for, other things being equal, selection will not stop until their differences are sufficient to eliminate confusion.

This pressure for divergence, resulting from speciation and the subsequent mingling of its products, has resulted in a wide variety of signal patterns among acoustic and visual insects; chemical signals must vary similarly, but no large number of them have been analyzed for comparative purposes.

Several kinds of parallelism in pattern evolution can be glimpsed from comparative work, particularly on acoustic signals. Evidently, similar pattern series have evolved independently and, in some cases, on different continents (Alexander, 1960) and between sympatric

cricket subfamilies with carrier frequencies so different that confusion is minimal because of the differential "tuning" of the auditory tympana of the different groups. Some close parallels exist between signal patterning in fireflies and acoustic insects (Alexander, 1960; Lloyd, 1966; Barber, 1951) (Figs. 2 to 5).

A parameter in the flashes of male fireflies that cannot be duplicated in acoustic signals is introduced by distinctive flight patterns during the flash (Fig. 4). Some males always swoop so as to make J-shaped flashes; others waggle the abdomen, in effect either pulsing the flash or at least modulating its intensity (Lloyd, 1966). Lloyd (1965b) also describes spatially patterned glowing organs on female fireflies and click beetles and reports that, in the latter case, males "can be attracted to an illuminated decoy with a twin light arrangement which simulates the prothoracic light organs possessed by both sexes, but not to a single light." These variables, together with variations in flight speed
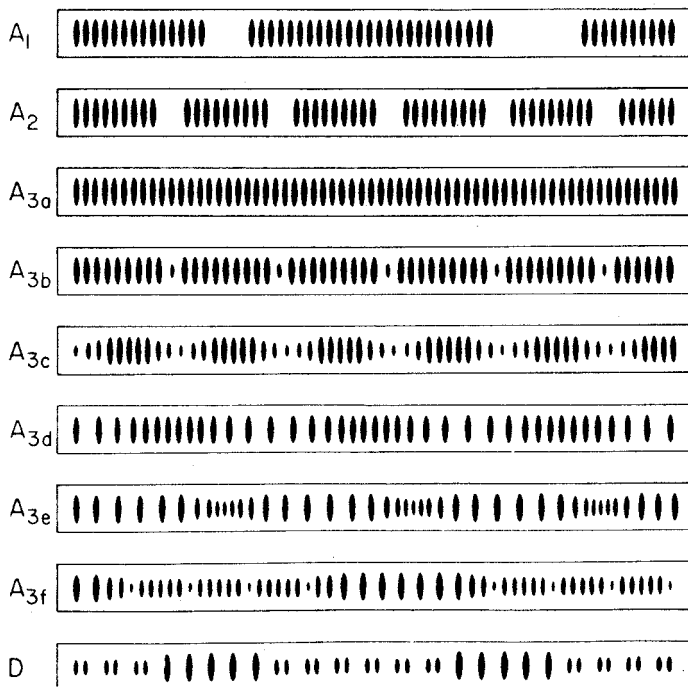

Fig. 2. Trilling pulse (wingstroke) patterns in calling (pair-forming) signals of male crickets. Vertical width changes indicate intensity fluctuations. Nomenclature is that of Alexander (1962). *Gryllus* species with A_1, A_2, and A_{3a} calling patterns have A_1 or A_2 aggressive patterns. Wingstroke patterns in A_{3a} sounds can be either open-close-open-close (etc.) or open-close-hold-open-close-hold (etc.). In crickets, wingstrokes are usually acoustically effective only during the closing part of the stroke.

during flashes, greatly complicate the problems of describing, analyzing, and reproducing firefly flashes.

Acoustic and visual signals of arthropods can be divided into two classes: those in which the signal pattern of one individual carries all the species distinctiveness and those in which the timing of responses between individuals is species-specific. The second case is common in fireflies, katydids (Phaneropterinae), and, to a lesser extent, grasshoppers (Acridinae); it relieves the pressures that in other groups have resulted in some extremely complex signal patterns; for the most nondescript sound can function in a species-specific fashion if its timing is critical. Apparently as a consequence, many katydid males produce quite simple lisps (Spooner, in press; Alexander, 1960; Spooner, 1964), and their females reply with even simpler, soft ticks. That this explanation is by no means complete is revealed by the
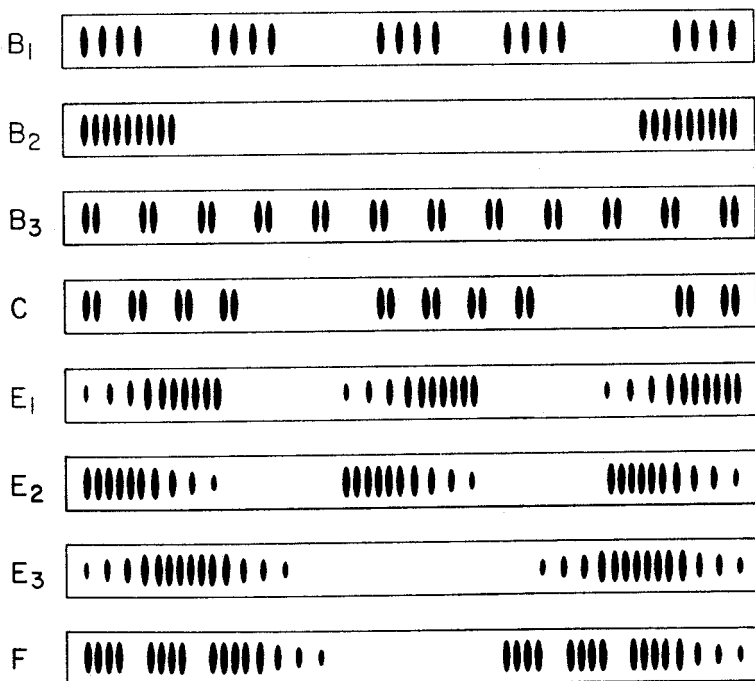

FIG. 3. Chirping pulse (wingstroke) patterns in calling (pair-forming) signals of male crickets. Vertical width changes indicate intensity fluctuations. Nomenclature is that of Alexander (1962). *Gryllus* species with B_1 patterns (includes all *Gryllus* and *Acheta* species studied neurophysiologically to date) have A_1 aggressive patterns; those with B_2 calling patterns both shorten chirp intervals and (slightly) lengthen chirps to make aggressive sounds; those with B_3 calling patterns have C aggressive sounds; those with C calling sounds shorten groups of chirps and intervals between groups of chirps to make aggressive sounds. None of the other patterns is known in *Gryllus* species.
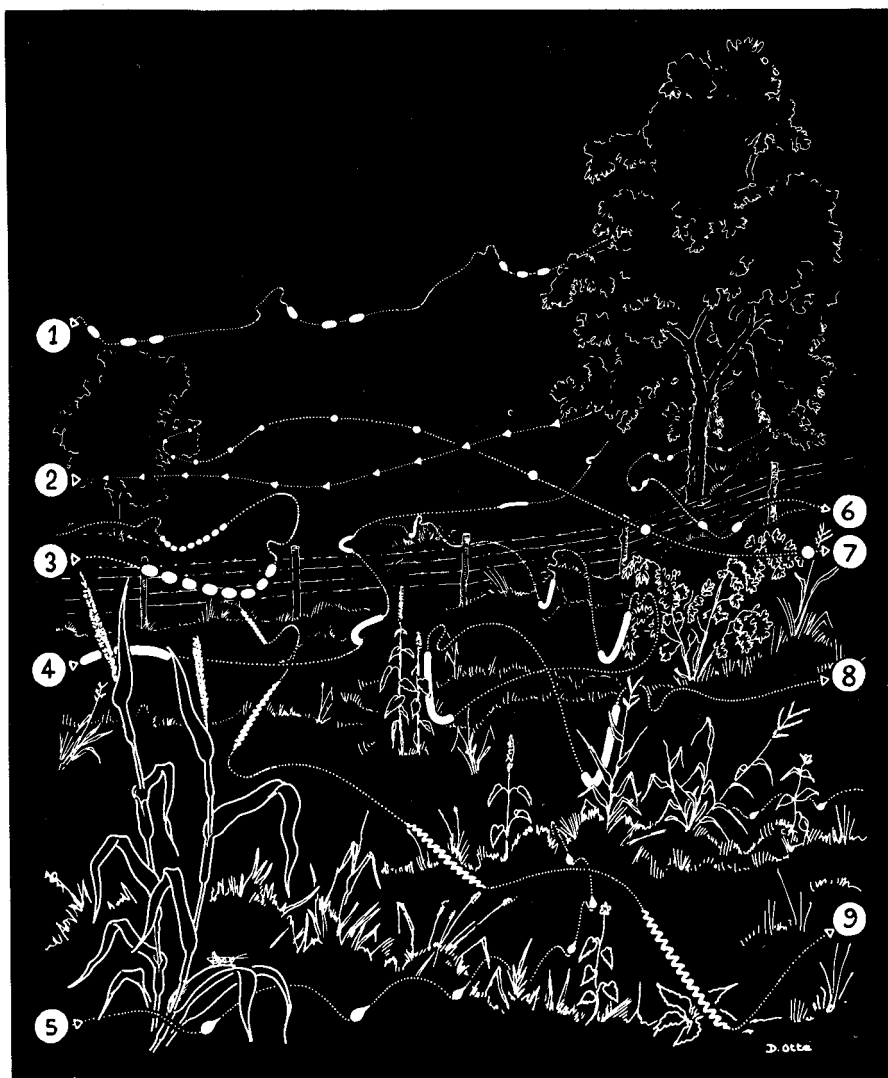
FIG. 4. Pulse (flash) patterns and flight during flashing in male fireflies of the genus *Photinus* as they would appear in a time-lapse photograph (modified from Lloyd, 1966). The species illustrated are not all sympatric. Small triangles near numbers designating species indicate direction of flight: (1) *consimilis* (slow pulse), (2) *brimleyi*, (3) *consimilis* (fast pulse) and *carolinus*, (4) *collustrans*, (5) *marginellus*, (6) *consanguineus*, (7) *ignitus*, (8) *pyralis*, and (9) *granulatus*.

presence in some Phaneropterinae of the most complicated of all arthropod sound patterns (Alexander, 1960; Spooner, in press).

Figures 1 to 5 show signal patterns in the calling signals of various crickets, katydids, grasshoppers, cicadas, and fireflies. These patterns bring up related questions concerning neurophysiological mechanisms and communicative significance: How does a particular signal pattern appear in a particular species? By what sorts of steps do signals change when species diverge? How much of a particular repetitive pattern is necessary to transmit the entire message? What is the significance of each part of a nonrepetitive pattern? What is the relationship between signal structure and input and output in the central nervous system? Are there correlations between functional communicative units and neurophysiological backgrounds?

In general, groups of closely similar species have the same signal pattern, with rate differences within the pattern giving species distinctiveness. Often a group of similar species show various gradations from one pattern to another, such as *Gryllus veletis* (B_1), *G. vernalis* (B_1–B_3), and *G. fultoni* (B_3); related species may have similar patterns, but not the same one, as with two quite similar western United States *Gryllus* species (B_3 and C). By comparing a wide variety of patterns, and other similarities and differences among species, it is

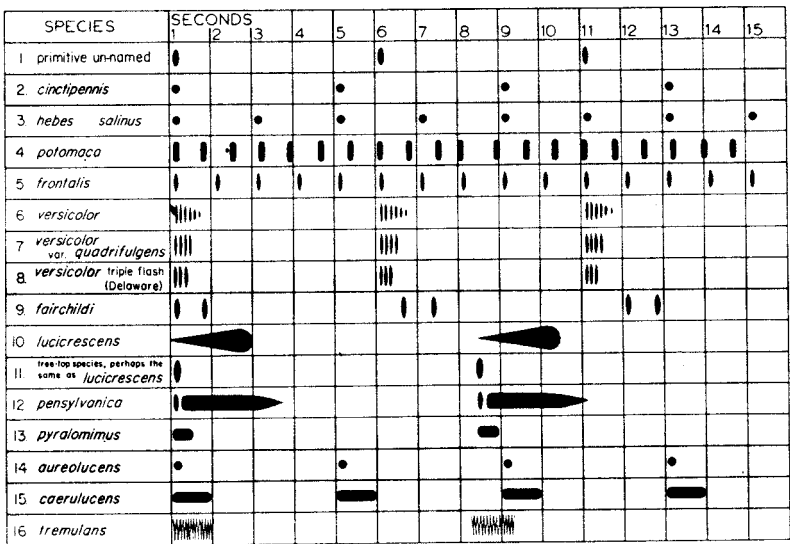| SPECIES	SECONDS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. primitive un-named															
2. cinctipennis															
3. hebes salinus															
4. potomaca															
5. frontalis															
6. versicolor															
7. versicolor var. quadrifulgens															
8. versicolor triple flash (Delaware)															
9. fairchildi															
10. lucicrescens															
11. tree-top species, perhaps the same as lucicrescens															
12. pensylvanica															
13. pyralomimus															
14. aureolucens															
15. caerulucens															
16. tremulans															

FIG. 5. Pulse patterns during flashing in male fireflies of the genus *Photuris* (modified from Barber, 1951). Species 2 and 14, with the same flash pattern, are quite different morphologically, were taken in Maryland and Minnesota, respectively, and may be allopatric. Delay times in female answers may be different between species.

possible to arrive at reasonable assumptions about some of the routes of change in song patterns (Alexander, 1962). As neurophysiological information becomes available and the nature of the communicative units (morphemes) in each pattern becomes clear, we should understand better why particular changes have occurred in particular cases.

I have tried to approach the answers to the above questions as closely as possible in the following passages, which deal with them in approximately the order of their presentation. Much of the information utilized concerns crickets; for this family has been most extensively studied in these regards.

DEVELOPMENTAL INFLUENCES ON SIGNALS AND RESPONSES

Vertebrates are so frequently used as a point of reference in behavioral discussions, even by invertebrate zoologists, that it may be useful to begin this comparison with a few general remarks about differences and similarities between arthropods and vertebrates. These two groups represent evolutionary lines in which not only the general organization of behavior but also the neuromuscular machinery upon which even relatively simple activities are based have evolved independently (Vowles, 1961). Their common ancestor was a worm-like animal, with relatively little centralization of the nervous system, which communicated only tactually and chemically, and which must have had relatively simple behavior in most regards. Evolutionary divergences between the two groups, in the face of their parallel tendencies to increase persistently the complexity of their behavioral organization, are remarkable. Adult vertebrates are characteristically long-lived, mate repeatedly, often have some kind of important parent–offspring interactions, and develop through juvenile stages that gradually transform them into adults, with respect to behavior as well as morphology. Their behavior is typified by the kinds of neurophysiological phenomena that we have labeled learning, memory, practice, tradition, and culture. In contrast, arthropods have elaborated their particular kinds of behavioral complexity while concomitantly emphasizing (for the most part) short adult lives, no generational overlap, and complex, and often rapid, metamorphosis in which few juvenile activities can easily be related to anything the adults do. One result is extreme examples of behavioral complexity relative to simplicity of eliciting stimuli and easily traceable developmental or maturational changes and directness of relationship between behavioral differences and genetic differences. One might predict that if some sort of extreme is ever to be exemplified in this regard—and we may note that this is the kind of extreme that "instinctivists" have

always been seeking and using as their mythical "base line"—it will be found in an arthropod.

With the exception of a relatively few social species such as wasps, bees, ants, termites, and some arachnids and crustaceans, most arthropods have no chance to hear or see the communicative signals of their parents or other members of preceding generations. This is particularly true in temperate climates where only a single stage, often the egg, is able to overwinter. Each year, countless individual arthropods grow up and begin to signal without contact of any kind with other members of their own species: this particular kind of isolation test, therefore, is performed repeatedly without assistance from biologists. In contrast, nearly all birds and mammals associate with their parents, and, in many respects, behave similarly to them during times when they are signaling visually and acoustically; even adult frogs and toads are likely to hear the calls of some surviving members of previous generations.

Acoustic insects not only grow up with little or no chance to hear the calls of their own species, they are also surrounded by a multitude of other sounds that bear little or no resemblance to signals they must eventually produce. A high percentage of the individuals in such species probably hear only totally foreign or inappropriate noises, and their own signals, during most or all of their lives, particularly during that portion of their lives when their ability to make the right noises in the right situation is developing.

These facts indicate that the differences between the ontogenetic flexibility of arthropod and bird and mammal noises is not owing simply to the evolution of flexibility in the vertebrates: in arthropods there must have been intensive selection for resistance to all kinds of acoustic influences, for nearly any that might be encountered could only change the ultimate nature of their acoustic signals in the wrong way. It is not surprising that, in general, the communicative signals of arthropods do not depend in any way for their structure on perception of the signals of other individuals, of either the previous or the same generation.

The next question one is inclined to ask is: To what extent is a signaling individual influenced by his own signals? Do arthropods improve with practice or repetition of signal-producing movements? We can begin the answer by studying the first signals produced by new adults, for all of the signaling systems compared here are essentially or completely restricted to the adults (the exceptions are three: that some firefly larvae can glow, but do not flash; that no one is certain at what ages the auditory organs of crickets, katydids, and grasshoppers actually become functional; and that juvenile grass-

hoppers may move their hind legs in fashions similar to those causing stridulatory noises in the adults.) Figures 6 and 7 present the first acoustic signals of cricket and cicada individuals reared in the laboratory, without the influence of any sounds resembling those of their own species; the sounds of older individuals of the same species are essentially the same. Numerous field observations, however, indicate that in some species of both Orthoptera and fireflies there is noticeable change in the signals. Lloyd (1964) indicates (and has
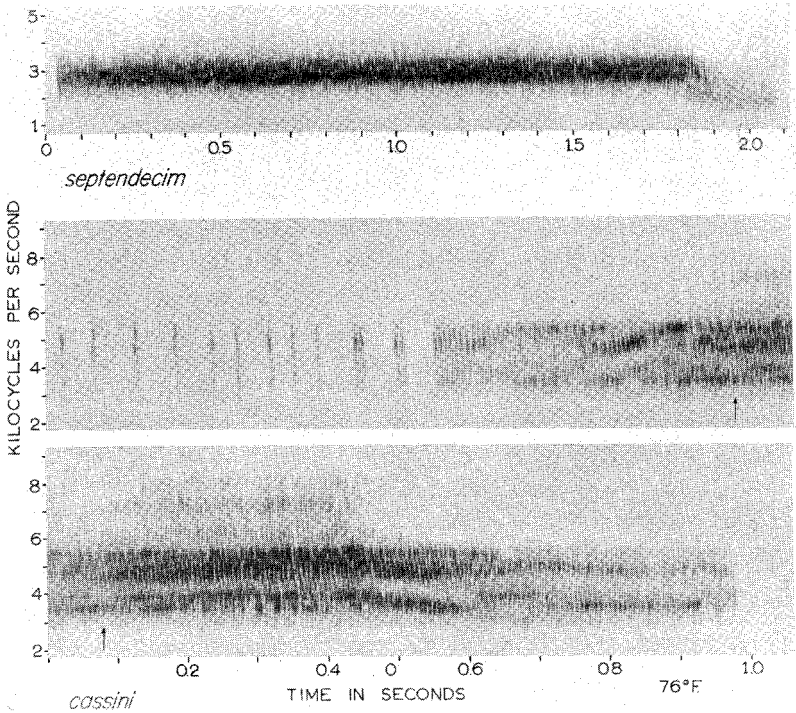
Fig. 6. Audiospectrographs of the first sounds of two periodical cicada males that matured alone in the laboratory, evidently normal in all respects.

shown me in the field) that, on the first evenings of flashing, males in firefly populations are more erratic than later in the season; they show more variability in such things as flight patterns, length of flashes, and number of flashes per burst. The same thing seems to happen in certain Orthoptera, most notably the true katydid (*Pterophylla camellifolia*) (Shaw, 1966). This katydid not only produces chirps that are more consistent in length after it has been chirping for a few evenings (in the north most often settling on consistent disyllabic chirps after producing

chirps with from one to eight or ten pulses), but the males also seem to become more discriminating in the nature of sounds to which they will respond (1) by timing their chirps (as in their normal alternation or antiphony) and (2) by beginning songs when they had not previously been chirping. But this katydid is unusual in another regard: the length of its chirps is affected by the length of chirps (artificial or produced by another katydid) with which it is alternating. Pierce (1949), Alexander (1960), and Shaw (1966) were able to secure three-, four-, and five-syllable chirps from males that ordinarily produced chiefly two-syllable chirps by playing chirps of these lengths antiphonally. This reaction seems to be a rebound effect from the inhibition caused
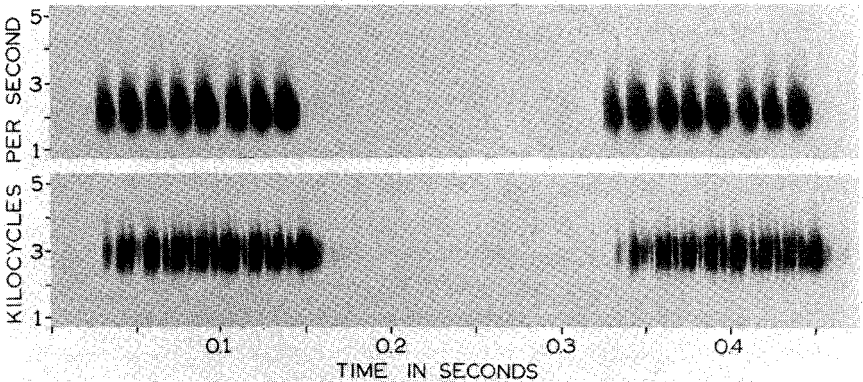

Fig. 7. Audiospectrographs of a normal song (*top*) of a male snowy tree cricket recorded outdoors (75°F) and that of a male deafened while still a juvenile and before hearing any tree cricket sounds (*bottom*) (76°F).

by increased lengths of simulated chirps; the reaction is somehow related to a close-range antiphony (that probably should be called aggression since there is evidence that it usually ends with one male stopping song and moving away) in which chirps with as many as thirty syllables have been recorded (Alexander, 1960). Nevertheless, different colonies of this katydid have different mode chirp lengths, and Shaw (1966) believes that the mode chirp length of an individual may be modified by long exposure to unusually short or long chirps. Isolated males seem most prone to develop disyllabic chirps, and one of Shaw's males with a mode chirp length of three syllables became a disyllabic chirper when caged near a male with a disyllabic chirp.

Only one other instance of possible permanent or long-term change in an arthropod's communicative signals by exposure to signals in

the same sensory modality has been reported, and that is Broughton's (1965) belief that a male of *Platycleis sabulosa* produced a sound unnatural for that species, and resembling a signal of *P. affinis*, after being caged for a long time with a male of the latter species.

Two investigators have described results indicating inability of females to respond to any calls but those of their own males. Walker (1957) purposely used in tests on song responses virgin female tree crickets (*Oecanthus nigricornis* and *O. quadripunctatus*) that had never heard any cricket song. Nevertheless, they discriminated between the calls of their own males and those of other species most similar to it. Haskell (1958) subjected female grasshoppers (*Chorthippus parallelus*) to various "wrong" noises during their last juvenile stages, and still could not make them respond to any sounds but those of their own males.

Several investigators have deafened old adult male crickets and noted that their ability to stridulate normally was not affected (Fulton, 1928; Alexander, 1960). Except for loss of ability to alternate or synchronize with other individuals, the only effects hinted have been tendencies to stridulate for either longer or shorter periods than nondeafened individuals, results which could be obtained if auditory feedback has a stimulative effect and if other noises picked up by the auditory organs are sometimes interruptive.

To my knowledge, no one has previously reported destroying an insect's auditory organs before they had become functional, thus before it could have heard any sound, and subsequently obtaining a song pattern from it. I tried this experiment unsuccessfully for several years with the snowy tree cricket (*Oecanthus fultoni*) because its chirps are so complex, and delivered at such an unvarying interval, and because the well-known mass synchrony of males in colonies suggests that auditory stimulation and auditory feedback are important. In August, 1965, I was finally successful, obtaining two sequences of chirps (208 and 272 chirps, respectively) from a male deafened as a juvenile (by cutting off its forelegs) before chirping began outdoors and one sequence (too far from the microphone to analyze) from another deafened while still soft after molting to adulthood. Chirps were recorded by using an automatic recording device in operation twenty-four hours a day for eight days. They were produced in sequences, at least as long and uninterrupted as those of normal males. Wingstroke rate, chirp length, and chirp interval were all normal, and chirp intervals following occasional short chirps were shorter, as in the singing of normal males. The chirps of the male in which individual pulses (wingstrokes) could be analyzed were abnormal in one unexpected regard: the stridulatory apparatus was in contact

during both opening and closing strokes of the wings, rather than just the closing strokes (Fig. 7). This defect did not disappear from this male's song during several hundred chirps. Intrachirp variations, however, are common in this species, the known ones including pulse groupings and pulse omissions or weak pulses; Walker (1957) found that females and males respond to pulseless electronic chirps if they are the right length and properly spaced. I doubt that the abnormality of this chirp would greatly reduce its communicative value to males or females, and I further suspect that it was not owing to the male's deafness but to thoracic damage caused by handling during deafening.

Evidently, all of the important communicative components of this sound are programmed to develop without the influence of acoustic stimuli. This interpretation would be incorrect in the case of the following rather remote possibilities: (1) significant input may have occurred through the severed auditory nerves, (2) the cerci may have transmitted significant vibrations, or (3) the subgenual organs on the middle and hind tibiae (homologues of the foretibial auditory organs) may have transmitted signals having the same effects as signals usually transmitted by the foretibial auditory tympana. Proprioceptive feedback influencing signal pattern seems unlikely, though not specifically tested in this species. In several other crickets I have observed that severing the wings completely so that only tiny stubs can be seen moving evidently does not alter the stridulatory pattern. This at least restricts the possibility of significant proprioceptive feedback to the muscles themselves.

With the exception of the true katydid and Broughton's reports on *Platycleis sabulosa,* the above evidence supports the idea that selection relative to developmental influences on signal structure in arthropod communication has prevented effects from stimuli in the same sensory modalities, a selective direction in contrast to that occurring on most parts of most signals of birds and mammals, though perhaps not too divergent from that responsible for the evolution of amphibian acoustic signals. The most we can say of a positive nature about developmental influences on communicative signals in arthropods is that, with a few minor and doubtful exceptions, not a single one has been discovered; no one has found any way, short of actual mutilation or gross physical deformity, to alter the communicative signals of any arthropod. Wherever the internal environment of the structures responsible for the ultimate patterns of these acoustic and visual signals may be, the variable inputs of the developing individual's external environment must be translated into an essentially constant, species-specific milieu before they reach it. In what ways has selection brought this about?

EFFECTS OF HEREDITARY VARIATIONS

Natural and experimentally produced hybrids between arthropod species with different communicative signals are known only in crickets, katydids, and grasshoppers. The results are important not only in assessing the influence of genetic differences upon signal structure but in attempts to understand how signals and responses to them have changed in the course of evolution, particularly during speciation. Unfortunately, not all of the results are easy to evaluate or interpret, especially when no objective analysis is available for the pertinent aspects of the signal patterns. However, since evidence of this kind is so sparse for any kind of behavior in any animal, it seems worthwhile to give a thorough, critical review here of all cases.

Fulton (1933) conducted perhaps the first experimental hybridization of two species with different songs, and his study is still the most careful and detailed analysis available. He hybridized two North American ground crickets, *Nemobius allardi* and *N. tinnulus*, sibling species that are adult at the same time and overlap both geographically and ecologically, the former an inhabitant of grassy areas, the latter a woodland species. Fulton was able to analyze the songs of F_1 and F_2 hybrids and F_1 backcrosses with both parental species (Fig. 8).

Both *N. allardi* and *N. tinnulus* produce simple trills or pulse successions during calling. Their calling songs differ almost solely in the length of the silent intervals between pulses. Evidently the length of these intervals alone was changed in the various hybrids (in spite of Marler's statement (1963, p. 288) that "song of the F_1 generation was intermediate between those of the two parents in several respects, including tempo").

The two species differ in the length of the stridulatory file and the number of teeth on the file (Pierce, 1949; Alexander and Thomas, 1959), and probably the individual pulses of *tinnulus* average somewhat longer than those of *allardi*; but no analysis specifically to test this question has yet been carried out.

Fulton's results are in most regards straightforward: pulses in the songs of F_1 hybrids were delivered at intermediate rates, those in the songs of backcross progeny were generally somewhat more like the parent used in the backcross when compared with one another. There are some puzzles, however. The pulses in both backcross hybrids seem too slow; two of them are slower than most recorded *tinnulus*, and all but one of both kinds of backcross hybrids have slower pulse rates than the F_1 hybrids. The F_2 hybrids also seem to

have pulse rates that are a little too slow—nearly all slower than the songs of the F_1 hybrids.

Two possible sources of error in the analysis could explain this discrepancy. First, Fulton·had no method of counting pulses except by ear and by using a vibrating clamp that he could set by ear to correspond with the speed of pulse delivery in the insects' songs. As
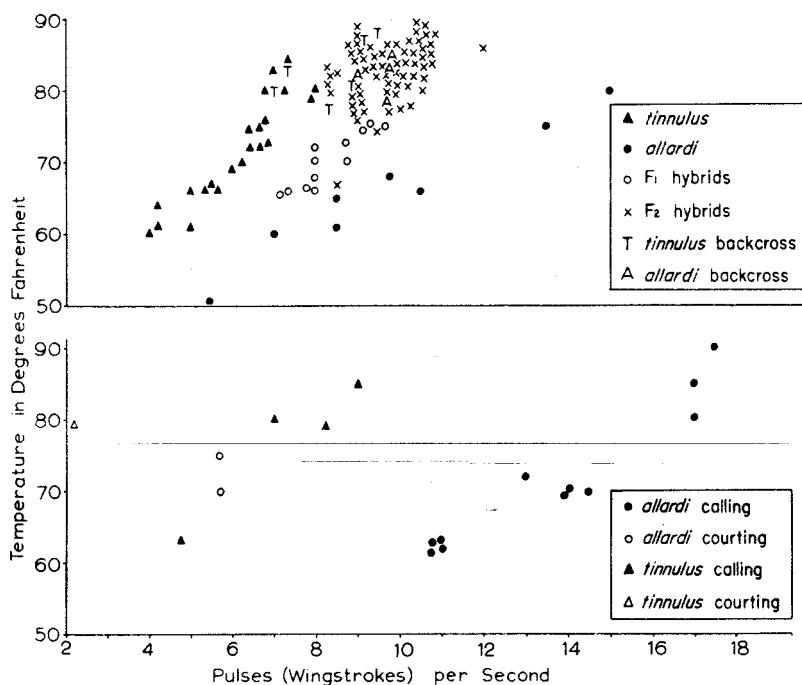

FIG. 8. Wingstroke rate differences (wing-hold interval differences) between two sibling species of ground crickets (*Nemobius*), between calling and courtship songs within species and among various kinds of hybrids. Data from Fulton (1933) (*top*: North Carolina) and Alexander and Thomas (1959) and Pierce (1949) (*bottom*: Ohio, Illinois, Indiana, Pennsylvania, New Hampshire).

he cautioned, his counts above six pulses per second are probably somewhat inaccurate, and many of the hybrid songs were evidently heard only at higher temperatures and therefore were more rapid and difficult to analyze.

The second possible source of error involves the relationship between courting and calling sounds of *N. allardi* and *N. tinnulus*. One of the courtship sounds of both species is simply a slowed version of the calling sound. The particular courtship sound in *allardi* is quite similar to the calling sound of *tinnulus*, so similar that the

insects themselves are probably unable to distinguish them. Some of the crickets whose songs Fulton analyzed may have been courting, not calling: he could have no way of telling certainly under all circumstances, and the possibility is especially great when large numbers of crickets are caged together as they evidently were in this case. With intermediate hybrid songs involved, the possibility of confusion is even greater.

Fulton's results deserve a little more discussion. The principal difference between the calling songs of these two species is the length of the interval between closing of the wings; this is the difference that hybridization indicates is controlled by more than one gene, and it is a difference that the insects themselves cause when they go back and forth between calling and courting situations. It would seem valuable to analyze the nature of the interval further, as well as the neural circuitry involved in the two different songs of each species. The interval between pulses could involve merely different rates of moving the wings back to an "open" position, ready to stroke acoustically again, but this does not seem likely. Moving pictures of calling *Gryllus* males and direct observations on courting *Nemobius* males indicate instead that the wings are returned to the open position very quickly, most probably at about the same speed in all songs, just as they are closed during stridulation at approximately the same rate in all songs. The rhythm is open-close-hold-open-close-hold, etc. What is varying between species and songs is a period of time during which the wings are held more or less motionless before stroking again. This "wing-hold" interval may very well be a simple inhibitory phenomenon.

Four other reports on the songs of interspecific cricket hybrids all involve field crickets in the genera *Teleogryllus* and *Gryllus*. Alexander (1957) reported that a field-collected male, sought out because its song seemed unique, is morphologically intermediate between the two species intermingled in that habitat, *G. fultoni* and *G. veletis*. The song (Figs. 9 and 10) has a pulse rate intermediate between these two species, four-syllable chirps like those of *veletis*, a regularity in chirp delivery reminiscent of *fultoni*, and a chirp rate intermediate between the usual chirp rates of *veletis* and *fultoni*. This is the only known example of a field hybrid between crickets with different songs.

Hörmann-Heck (1957) reported on four aspects of the behavior of hybrids between the two European field crickets *G. campestris* and *G. bimaculatus* De Geer: (1) amount of juvenile aggressiveness, (2) amount of antennal trembling during postcopulatory behavior, (3) whether or not the head and forebody were wobbled during cop-

ulation, and (4) the presence or absence of a specific sound (die *Anstreichlaute*) caused by lifting of the forewings from resting to stridulatory position just prior to courtship stridulation. She reported some kind of intermediacy in all cases except that all F_1 hybrids
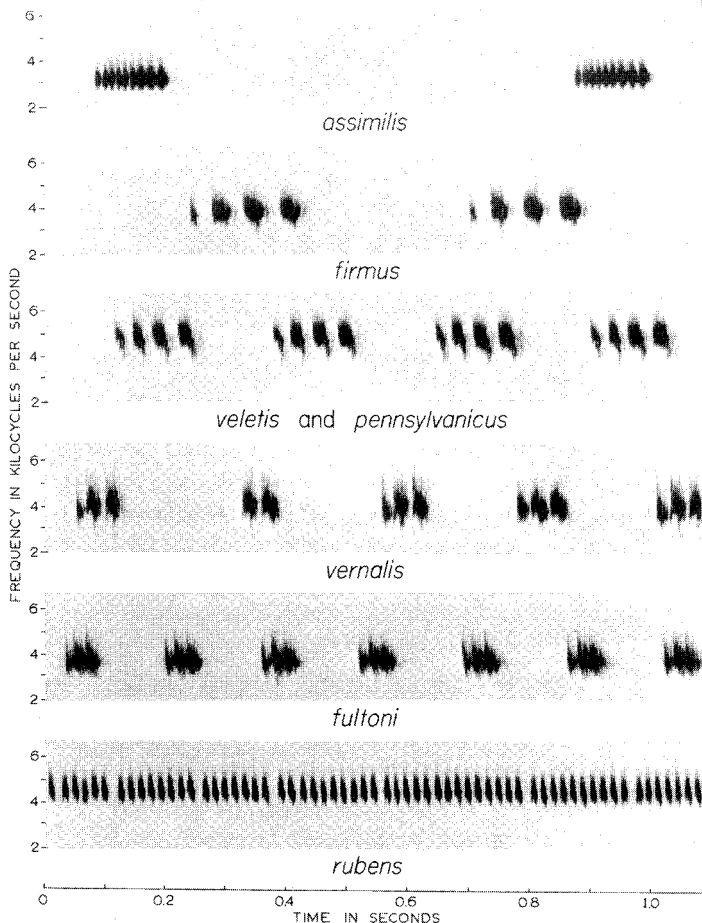

Fɪɢ. 9. Audiospectrographic samples from the calling songs of the field crickets (*Gryllus* species) of eastern North America (85°F).

trembled the antennae. Her findings were badly misinterpreted by Dilger (1962), the only author who has cited them in detail. Our main interest here is the effect of hybridization on courtship stridulation. I have reared both species in the laboratory and listened to their courtship sounds; I must report that I do not understand the difference

which Hörmann-Heck describes as follows: *bimaculatus* produces a sound during repeated lifting of the tegmina from resting to stridulatory position before beginning courtship stridulation; *campestris* lifts its tegmina only once soundlessly in this situation; most F$_1$ hybrids lift
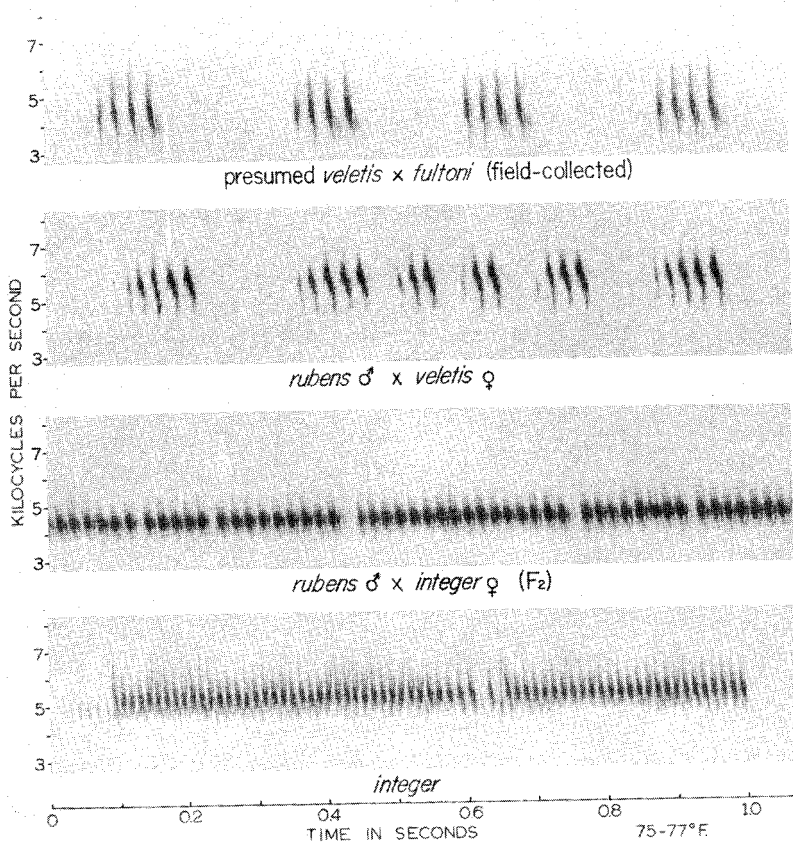

FIG. 10. Songs of hybrid field crickets and one parental species. *Top to bottom:* a field-collected presumed hybrid between *Gryllus veletis* and *G. fultoni* (40 pulses/sec); a laboratory hybrid between a *G. rubens* male and a *G. veletis* female (42 pulses/sec); an F$_2$ laboratory hybrid between a *G. rubens* male and a *G. integer* female (these two reared by R. S. Bigelow) (ca. 52 pulses/sec); *G. integer* (ca. 80 pulses/sec) (for comparison, see also Fig. 9; note temperature difference).

their tegmina once with sound, and a few behave like *campestris* or like *bimaculatus*. "Observations on F$_2$ and F$_3$ backcrosses proved that the transmission of this character can be explained, too, on a monofactorial basis" (p. 182).

The hybrids that I have described so far were all between chirping

species or trilling species. Bigelow (1960) reported hybrids between trilling species of *Gryllus* and also between chirping and trilling species (Fig. 10). When males of the chirping species, *G. veletis*, were crossed with females of the trilling *G. rubens*, Bigelow said (p. 510):

> The first hybrid song heard was a distinct trill followed by two chirps . . . Other hybrid males sang with a series of "trills," each approximately intermediate in length between typical *rubens* trills and typical [*veletis*] chirps. Unfortunately no tape recorder was available when these songs could be recorded and consequently the rate of wingstroke, etc., of these hybrid males is not known. The audible differences, however, between *rubens*, hybrid, and [*veletis*] songs was readily apparent to all who compared the three sounds.

The hybrids had file tooth counts almost exactly intermediate between those of the parental species and very likely had intermediate wingstroke rates. In another cross Bigelow obtained a male hybrid between a *veletis* female and a *rubens* male. The song (Fig. 10) was recorded at 80°F and contained 3 to 5 (usually 5) wingstrokes per chirp (like *veletis*), 230 to 240 chirps per minute (like *veletis*), and 5000 to 6500 toothstrikes per second (like both parental species). The wingstroke rate within the chirp is almost exactly intermediate between the rates of the parental species, about 25 per second for *veletis* and 60 per second for *rubens*.

Bigelow also crossed females of *G. assimilis* (a chirping species) with males of *G. rubens*. The hybrid males chirped and had wingstroke rates intermediate between the two parents (90 to 105 per second for *assimilis* at 70°F, 60 per second for *rubens* at 80°F, 75 per second for hybrids at 75°F). Bigelow concluded that the genes responsible for causing a field cricket to chirp are probably located on the X chromosome (♂ XO, ♀ XX). Those responsible for wingstroke rate variations are obviously not located on the sex chromosomes, since there was segregation of variations in these two characteristics as well as a probable difference in the number of genes involved in the differences between pulse rates and those between chirping and trilling. There is a suggestion here that song characteristics which stem from pacemakers located in different parts of the central nervous system have been altered by replacing genes located on different chromosomes. Since the difference between a chirping and a trilling song is simply a very long wing-hold interval which becomes the chirp interval, an interesting relationship exists with the findings of Fulton (1933) with trilling *Nemobius* songs having a very long pulse interval.

Species in the field cricket genus *Teleogryllus*, found in Africa, Asia,

Australia, and the South Pacific Islands, have complex calling songs consisting of trills and chirps interspersed or trills with two different pulse rates (Fig. 11). Probably these crickets have isolated the two functional parts of the calling song—attraction of females and re-pellence of other males—into two different rhythm units, as evidently have some meadow grasshoppers (Tettigoniidae: Conocephalinae) and cicadas (Alexander, 1960). Thus, *T. commodus* (Australia) and
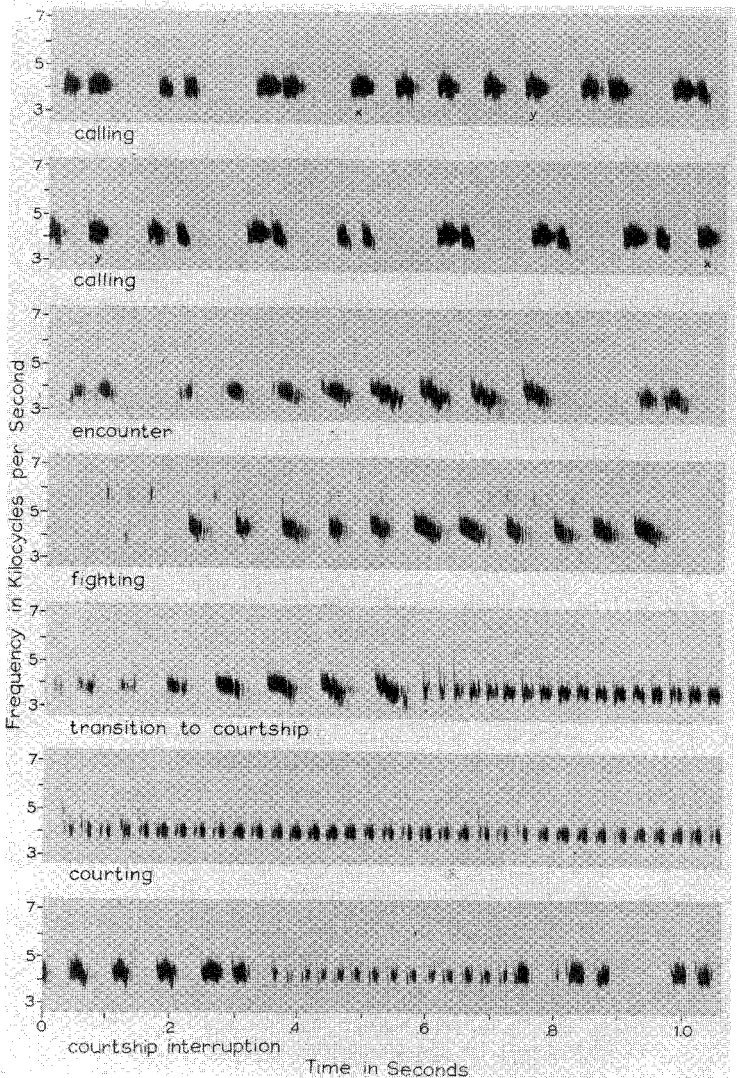

FIG. 11. Acoustic repertoire of *Teleogryllus commodus* from Australia, the most complex repertoire known in crickets.

two South African species studied in my laboratory all delete the chirping portions of their calling rhythms when they meet another cricket (the aggressive situation) and simply trill. A third rhythm is introduced by these species during courtship. *T. commodus*, therefore, has three different pulse (wingstroke) rates in its sounds: (1) 15 per second in the calling (aggressive) trill; (2) 25 per second in the calling (female-attraction) chirp; and (3) 35 per second in the courtship trill (75°F).

Leroy (1963) hybridized two species of *Teleogryllus* which she identified as *commodus* from Australia and *oceanicus* from Tahiti. She recorded the calling songs of seventy-two hybrid males and reports that all had the same rhythm. The song she illustrates for *T. commodus* is not the same as that taped in our laboratory (Fig. 11), which more closely resembles her oscillograph of the song of *T. oceanicus*. This problem of identification will have to await further information. (My material was secured from R. S. Bigelow, who reported its origin as Queensland, Australia.) At any rate, the two pulse rates in the calling song Leroy records for *commodus*, at 25°C, are 28 and 48 per second, those in the song of *oceanicus*, 20 and 32 per second, and those in the hybrid, 24 and 40 per second. Additionally, there is a group of pulses in the hybrid song, delivered at a rate of about 44 per second, located between the other parts of the song pattern. This she suggests is an additional rhythm unit not found in either parent, though the possibility seems not to have been eliminated that it represents a small bit of courtship stridulation. The chirps in the hybrid song are also longer than those in the song of *oceanicus* (three to five pulses as compared with two). The pulses in most of these rhythm units seem about as long as the pulse intervals; and when the intervals are longer, the pulses also seem longer, suggesting that pulse rate is a matter of the rate of movement of the wings and does not involve a wing-hold interval as postulated for *Nemobius* above; the same may be true for the trilling *Gryllus* species, *rubens* and *integer* (Figs. 9 and 10).

Pterophylla camellifolia (Fabricius) is the true katydid of eastern North America—the insect whose sound is responsible for the entire family Tettigoniidae coming to be called "katydids." It is a large, flightless, green insect that lives only in deciduous trees, generally calls only at night, and occurs from New England to Florida west to Wisconsin and Texas. Its calling phrases, or chirps, are not alike in all parts of this range, however (Figs. 12 to 15). In northern states the wingstroke rate is a little more than half that in southern states, and most chirps are disyllabic or trisyllabic; in southern states most chirps have at least four syllables, frequently as many as seven; from
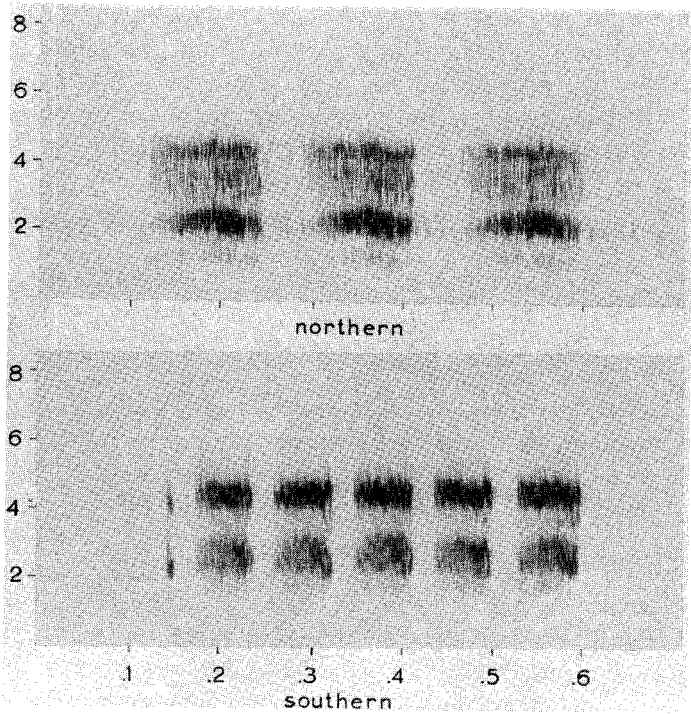
Fig. 12. Calling chirps of northern and southern katydids, showing the differences in pulse (wingstroke) rate and pulses per chirp.

Louisiana east to the Choctawhatchee River, and north through most of the length of the southern tier of states, practically all chirps are disyllabic but have the very fast southern wingstroke (pulse) rate. With regard to wingstroke rate and chirp length, there is a zone of intergradation extending southward down the Appalachian mountains from New York City through Chipley, Florida, to the coast and west from near Atlanta, Georgia, through Missouri to form an inverted Y shape.

The male genitalia change in the same region, indicating a definite hybridization zone. This zone has been analyzed on the basis of recordings and auditory analyses of the songs of thousands of males in nearly all of its regions, sometimes through complete transects of recordings across the entire zone (Alexander and Shaw, unpublished). It varies in width from a few yards to more than a hundred miles, is sometimes abrupt with scarcely any evidence of hybridization, and at other times shows a smooth change in all characters involved (Figs. 13 to 15). There can be no doubt that wingstroke rate differences depend on a genetic difference between northern and southern pop-
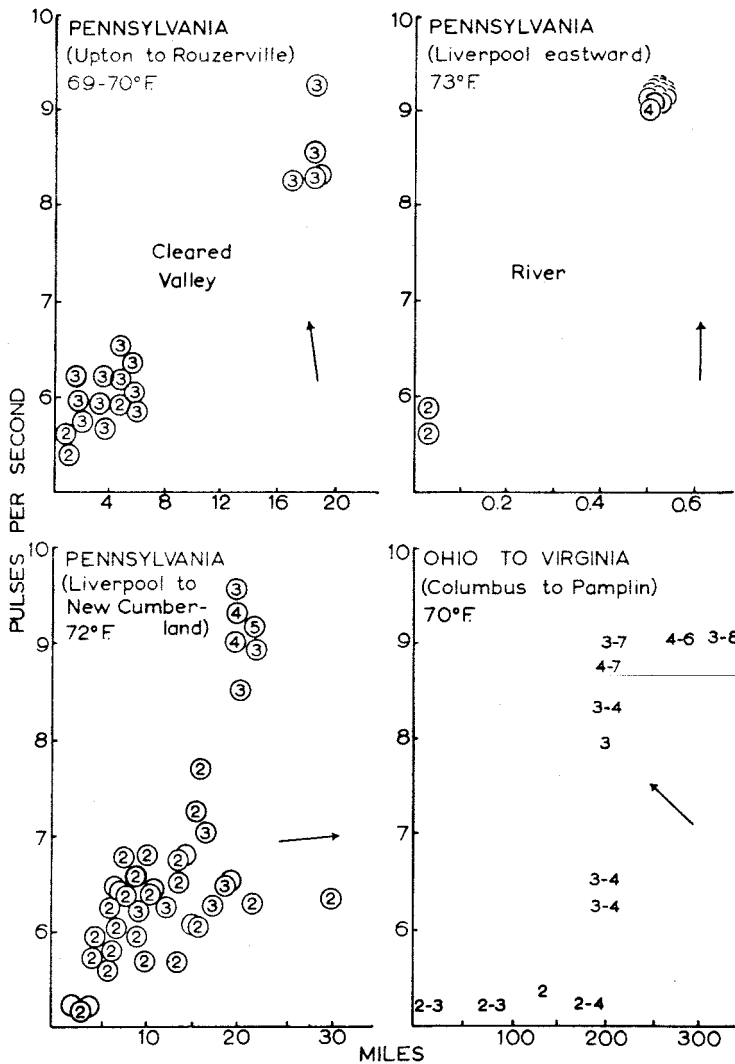
FIG. 13. Field records of song change in various locations along an Appalachian zone of hybridization between northern and southern katydids. Numbers in circles indicate mode number of pulses per chirp (deviations from mode are rare). Symbols stacked together indicate a chorusing population, songs all alike. Lower right shows how the song change is localized in the Appalachian region. Upper right shows pure populations on either side of the Susquehanna River in Pennsylvania (a precivilization barrier); upper left shows influence from both populations on the two sides of a cleared field (a postcivilization barrier). Arrows indicate north. Lower left shows intergradation.
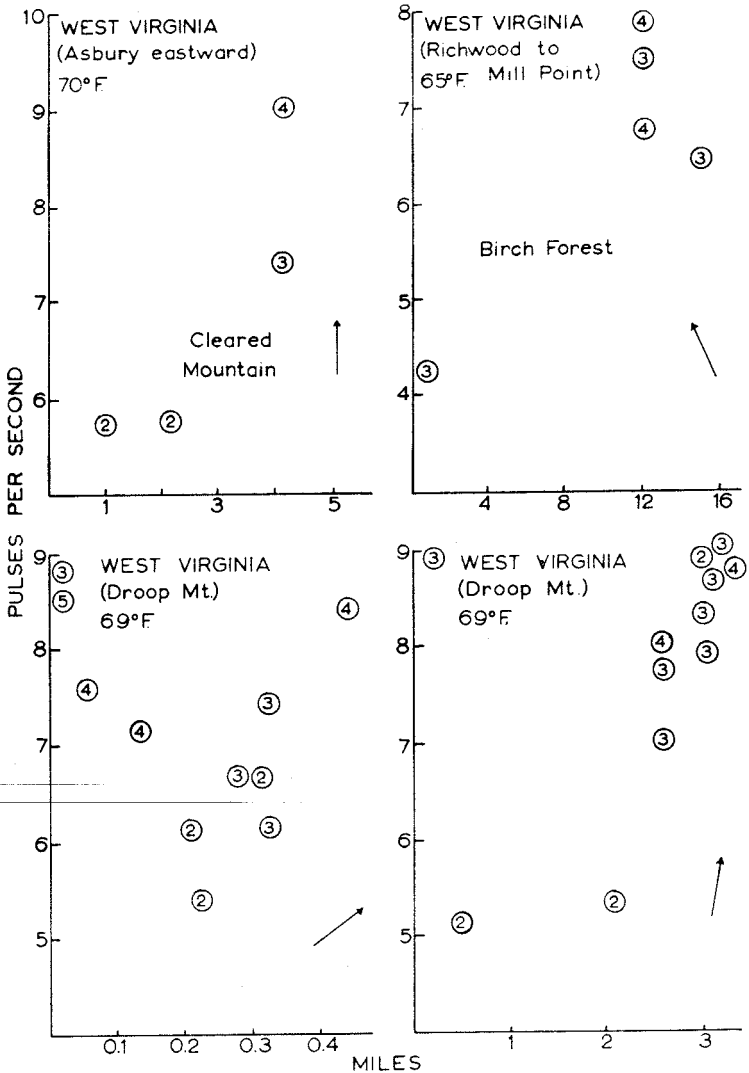
FIG. 14. Field records of song change in various locations along an Appalachian zone of hybridization between northern and southern katydids. Numbers in circles indicate mode number of pulses per chirp (deviations from mode are rare). Upper right shows effect of birch forest, a precivilization barrier. Upper left illustrates a postcivilization barrier. Lower left and right show a northern population surrounded by southern katydids and intergrading with them along roads running in four directions from the center of the colony. Arrows indicate north.
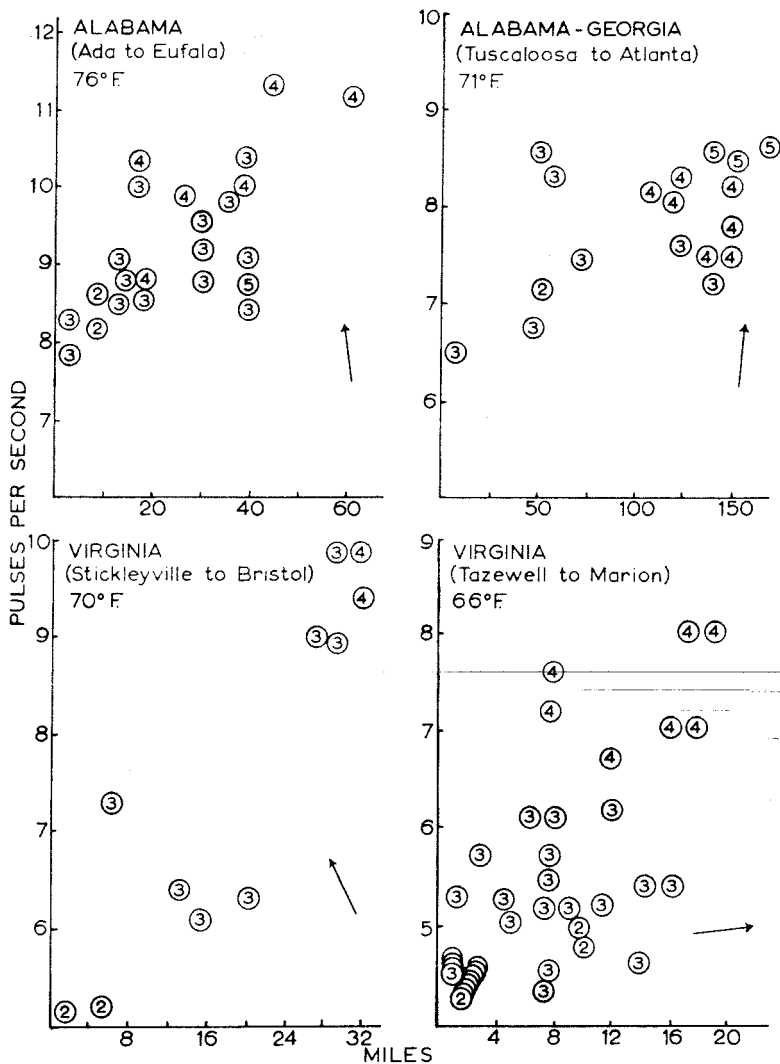
FIG. 15. Field records of song change in various locations along an Appalachian zone of hybridization between northern and southern katydids. Numbers in circles indicate mode number of pulses per chirp (deviations from mode are rare). Symbols stacked together indicate a chorusing population, songs all alike. Arrows indicate north.

ulations involving several genes. The basis for chirp-length variations, however, may be more complicated. Shaw (1966) has shown that for northern and southern wingstroke rates there are different optimal lengths for the chirps—two syllables in the north and four syllables

in the south. This "optimal" length is the length at which, given the chirp interval possessed by these katydids and the particular timing of the central nervous system circuit involved in their antiphonous (alternating) chorusing, neighboring males can alternate with the least chance of disruption. Since, as discussed earlier, a male's chirp length can be adjusted, perhaps permanently, by the length of an antiphonous chirp, it is possible that part of the north–south variations in chirp length are caused with no genetic differences other than those affecting wingstroke rate: a katydid with a given wingstroke rate may have a propensity to develop a chirp with a particular length. The chirp length differences between southeastern and Louisiana katydids, however, probably could not be explained this way unless there is also a variation in the length of the chirp interval.

This case involves interesting questions concerning when communicative signals change during speciation, and why. Evidently, song divergence in *Pterophylla* preceded sympatry between geographically isolated populations that did not acquire reproductive barriers while apart. What selective action caused the changes? There are no species in the same subfamily, or apparently with remotely similar sounds, except in Florida, where the similar genus, *Lea*, overlaps southeastern *Pterophylla*. A second question, still unanswered, is whether or not in some regions the song difference, or other barriers, is reducing or even preventing gene flow. In some localities along the hybridization zone, the two song forms live side by side with scarcely any evidence of hybridization. But they do not overlap. There is no information concerning which parts of the song are essential in attracting the female. Curiously, the only species with a strong hint of modifiability in its song pattern by acoustic stimuli is also the only one showing extensive hybridization in the field between forms with strikingly different sounds.

Perdeck (1958) has carried out by far the most widely cited study of hybridization between two species of arthropods with different songs. He hybridized two sibling species of grasshoppers, *Chorthippus brunneus* Thnb. and *C. biguttulus* L. The male calling songs of these two species differ in the length and spacing of pulse groups (Perdeck's "notes"): *brunneus* notes are less than $\frac{1}{3}$ sec long and delivered in groups of two to thirteen at a rate of about one in 2 sec; *biguttulus* notes are 1.19 to 4.6 sec long and delivered in groups of one to five at a rate of about one in 3 sec. A hybrid phrase (or chirp) plotted by sound level has six notes, each about $\frac{2}{3}$ sec long, and delivered at a rate of about one in 2 sec. Length of notes, and number per phrase are thus intermediate in this hybrid, but the note rate is actually a little faster than in the song of the faster species, *brunneus*. Temperature is given

as "about 35°C." Other data on hybrid songs are given in tables, but interval lengths are omitted, so that only the more variable aspects of the songs can be compared. In two of five characteristics compared —"main pulses" per second and "main pulses" per "note" (legstrokes per second and legstrokes per note)—the hybrids actually fall outside the range of variation of the two parents combined.

Since Perdeck did not use virgin females in his test, but instead used field-collected adults of unknown history, it was necessary for him to identify hybrids by their songs. He described additional differences, less easy to quantify, between the aggressive and courtship sounds of the parental species.

NEUROPHYSIOLOGICAL MECHANISMS

What is known concerning the neurophysiological mechanisms underlying signals and responses in these communication systems in which developmental influences are so cryptic and hereditary differences so directly reflected in the phenotype? Although we are far from a reasonable understanding, much work has been done recently, chiefly with crickets, providing a story unparalleled in detail and completeness.

The general picture of the acoustic system of a cricket or katydid is shown in Fig. 19. Sound enters via the tympana on the forelegs. These tympana are most sensitive to vibrations across the frequency spectrum dominant in the species' sounds (Wever and Vernon, 1959); in crickets this is almost a single frequency, in katydids a more or less wide spectrum. The auditory nerve is probably able to fire faster than the fastest pulse rates known to be produced by Ensifera (250 to 300 pulses per second in certain bush crickets in the subfamily Eneopterinae), so that analysis of rhythm patterns takes place in the central nervous system. Suga (1963) has traced the auditory nerve of several crickets to the prothoracic ganglion; presumably, its connections to the CNS there resemble those of katydids. Suga and Katsuki (1961a, b) reported that the auditory nerve of the katydid *Gampsocleis burgeri* transmits information to the prothoracic ganglion and then, after a delay of about twelve milliseconds, simultaneously to the brain and the metathoracic ganglion. They found evidence of inhibitory interaction between the left and right tympanic nerves, suggesting a CNS role in sharpening information relating to intensity differences on the two sides of the animal, thus accentuating the already considerable directionality of the tibial receptor system. Suga (1963) reported that the tympanic nerve in crickets, in contrast, weakly activates contralateral central neurons.

In crickets and katydids, acoustic input can stimulate stridulation, inhibit it, or change its rhythm; the significant variables, besides pattern differences, are intensity differences (Spooner, in press; Alexander, 1960, 1961) and timing with respect to the responding individual's own stridulatory cycle (Shaw, 1966; Jones, 1966a, b). Tactual input through the antennae stops calling stridulation and can start or stop aggressive stridulation; visual input can have similar effects (Alexander, 1960, 1961; Shaw, personal communication). Tactual stimulation of the cerci induces courtship in calling, silent, or even aggressive male crickets (Alexander, 1961). Possibly chemical stimuli impinging on the antennae, cerci, and maxillary and labial palpi, or all of these organs, may also affect some of these behaviors, particularly the onset and continuance of courtship stridulation.

Recently, Hüber (1965a, b), Ewing and Hoyle (1965), and Bentley and Kutsch (1966) have investigated muscular and nervous activity underlying stridulation in *Acheta domesticus* and various *Gryllus* species. Bentley and Kutsch list nineteen muscles in the mesothorax which operate in three groups, openers, closers, and raisers or positioners of the wings; the different positions and movements of the forewings result in three kinds of pulses, one occurring in calling and aggressive signals and two restricted to courtship singing; their findings with *Gryllus* concerning the functions of individual muscles differ radically from those of Ewing and Hoyle with *Acheta*, a closely similar genus.

Excluding a few highly complex patterns, there are two prominent kinds of sound patterns in the calling stridulations of crickets, known as chirps and trills. Trills are steady successions of wing openings and closings; chirps have wing-hold intervals, in most cases every two to ten pulses. Based on the above discussion of *Nemobius* songs, it would seem that two kinds of wing movement patterns also occur in trills, making three patterns of movement responsible for these two general kinds of sound patterns, as follows:

1. Chirp: *Gryllus firmus, G. veletis, G. pennsylvanicus, G. bimaculatus, G. campestris, Acheta domesticus.*

   Wing rhythm: open-*close*-open-*close*-hold-open-*close*-open-*close*-hold-repeat. This represents two two-pulse chirps produced in a fraction of a second. Acoustically effective portions of wingstrokes are underlined. Chirp interval is labeled "hold."

2. Trill 1: *Gryllus rubens, Oecanthus nigricornis, others.*

   Wing rhythm: open-*close*-open-*close*-open-*close*-open-*close*, etc.

3. Trill 2: *Nemobius allardi, N. tinnulus.*

   Wing rhythm: open-*close*-hold-open-*close*-hold-open-*close*-hold, etc.

Not much latitude in pulse rate would seem possible (for species differences) in the first kind of trill, since the principal limiting factor would be the extent to which rate changes could be effected in the actual speed of motion of the wings (distance traveled per unit time) during opening and closing strokes. One additional flexibility can be superimposed, however—changes in the length of the strokes. Walker (1962) found that as temperatures increase, and wingstroke rates correspondingly increase, some trilling crickets shorten their wingstrokes, using fewer teeth on the stridulatory file. This could be caused by the contraction speed of the muscles being too slow to draw the wing as far before the reversal of direction of stroke begins or by shorter trains of motor impulses to the wing muscles which, as in cicadas (Hagiwara and Watanabe, 1956), result in briefer bursts of muscle activity (Bentley and Kutsch, 1966). In species that evidently have this kind of wing motion, such as members of the *Gryllus rubens* and *Oecanthus nigricornis* groups, faster trillers as a rule have shorter files and shorter wingstrokes. Changes in the firing rate of a pacemaker responsible for wingstroke rate may be one of the first song changes during species divergence, followed by increases or decreases in file length, depending on the direction of change.

One of the interesting problems encountered by Walker (1962) was the lack of correspondence between changes in wingstroke rate (strokes per second) and frequency (cycles per second) of the sound, even though the latter clearly depends upon the number of teeth struck per second. He was able to show that shortened wingstrokes at higher temperatures account for part of the discrepency and that different rates of change in the opening and closing parts of the wingstrokes, respectively, account for the rest. In the latter case, there is evidently enough friction during the closing part of the stroke to retard its rate of increase in speed with higher temperatures and thus cause it to account for a higher proportion of the pulse interval time. Walker believed that selection must have favored pulse rate shifts which do not change the frequency of the sound, because it is most likely that temperature (which also shifts pulse rate) has little effect on the frequencies to which the tibial tympana are most sensitive. This is probably true, but such changes may sometimes be the simplest kind to make, and thus be incidental to the beneficial effect on the song. In other words, to change the pulse rate of an "open-close-open-close" trill and maintain approximately the same frequency in the sound, perhaps only the firing rate of a mesothoracic wingstroke "pacemaker" need be adjusted, automatically causing a shorter stroke and changing the effect of stridulatory frictional drag.

I have already discussed the "open-close-hold" trill, but an addi-

tional comment is pertinent here. This is the likelihood that it is actually more similar, both communicatively and neurophysiologically, to chirping songs than to "open-close" trills. As with chirping songs, two pacemakers probably have to be involved, one giving the "open-close" part of the pattern, as in the first kind of trill, the other superimposing the "hold," a period of inhibition every two to ten wingstrokes. The idea, already expressed, that the two pacemaking functions are separate entities in chirping *Gryllus* species is reinforced by wingstroke rate remaining constant when both chirp length and chirp interval are adjusted by antennal, visual, or acoustic input, as well as by the evidence presented earlier that variations in these two rhythm elements segregate during hybridization tests. Rhythm elements emanating from the mesothoracic ganglion apparently are never varied to produce the different signals in a species' repertoire, regardless of their position in the structural or communicative hierarchy in the cricket's stridulatory pattern. Differences between signals within species' repertoires evidently stem from brain (or cercal ganglion) functions. But, in the *Nemobius allardi* group, wing-hold interval is involved in both intraspecific and interspecific signal variations; it may be determined in the brain, mesothoracic ganglion, or cercal ganglion, or by various combinations of pacemakers in these ganglia.

In the snowy tree cricket (Fig. 7), all elements in the song pattern show great constancy and (all but one, at least) are produced normally in isolated, deafened males. Chirp rate is adjusted slightly to achieve synchrony when males are chirping close together. Several undescribed Mexican species related to *O. fultoni* differ only in chirp length and rate, not in either pulse rate or stridulatory file length as do crickets with B_1 chirping songs; a similar difference occurs with *Gryllus* species having B_2 chirping songs (Alexander, unpublished). These findings are commensurate with Walker's (1957) discovery that snowy tree crickets do not use the pulse rate directly in communication; it is merely a carrier of chirp length and rate which the cricket, with its oscillatory stridulating device, cannot avoid producing. In these various crickets it would appear that only a "master" pacemaker affecting chirp (hold) interval (and chirp length) and supposed in other cases to be located in the brain (or perhaps in the prothoracic ganglion, see explanation for Fig. 19) has been changed to produce species differences in calling songs. In these B_2 song patterns, pulse rate is usually very fast and aggressive sounds (*Gryllus* species) are made by changing the chirp interval rather than its length. Pulses have been relegated to the role of "subphonemes," the entire chirp, perhaps including its interval in some cases, being roughly equivalent to a pulse in the B_1 song and making up the morpheme (smallest

information-carrying unit). In B_1 songs the morpheme is a short pulse group, perhaps no more than two pulses in length.

In all species treated so far, wingstroke rate differences between species seem to depend on a number of genes, while differences in patterning of wingstrokes (chirp patterns) may depend on a different gene or genes located on another chromosome (Bigelow, 1960). It is within reason that discovery can be made of the number of genes involved in pulse rate differences between species and the quantitative effect of single gene replacements on pulse rate. Such information, together with studies of variation within species, is needed to elucidate how overlapping genetic differences between incipient species become effective in selective divergence.

In a series of publications, Hüber (1955–1965) has discussed his findings that certain of the sounds in a field cricket's repertoire, and also a more or less nonacoustic wing-whirring prominent in some *Gryllus* species (preflight behavior), can be produced by stimulating the cricket brain and that brain stimulation in different regions causes different kinds of sound or wing motion. There has been one major misunderstanding, and that is the belief that Hüber has elicited courtship sounds by brain stimulation (Roeder, 1963; Ewing and Hoyle, 1965). True courtship is normally carried out only when the cerci are bing stimulated (Alexander, 1961), and Hüber has not secured this sound during brain stimulation. Bentley (personal communication) was unable to elicit courtship by using cercal stimulation with the brain and prothoracic ganglion disconnected from the mesothoracic ganglion. The question remains whether courtship can be elicited by brain stimulation in the absence of cercal stimulation.

Hüber's findings have been widely interpreted as indicating centers in the brain for each of several different complex activities—different songs and preflight wing-whirring. Ewing and Hoyle (1965), after analyzing the differences in wing motion during calling, aggression, and courtship, concluded that no such postulate is necessary; but they found it necessary to invoke a "general inhibitor of F-axons [fast axons]" to produce courtship. They did not attempt to identify further or locate this "general inhibitor" function in cricket's central nervous system, but there seems to be no reason why it could not be a "separate neuronal center independently storing the information necessary to evoke [courtship]" (p. 150). Since Ewing and Hoyle postulate direct sensory influence in the change from calling to aggressive stridulation, they seem merely to have reduced the likelihood of "separate centers" from three to two. If information from the cercal ganglion is necessary for full courtship, we may eventually be referring to the cercal ganglion as a "separate center" in this system.

But Hüber did not obtain courtship stridulation from brain stimu-
lation anyway. There remains the question of precisely what sounds
he did obtain and how their structure relates to sensory input that
might be associated with the regions of the brain he stimulated. I
am indebted to Dr. Huber for permission to make and use here audio-
spectrographs from his recordings of normal and brain-stimulated
sounds of *G. campestris* (Figs. 16 to 18). Comparisons of these sounds
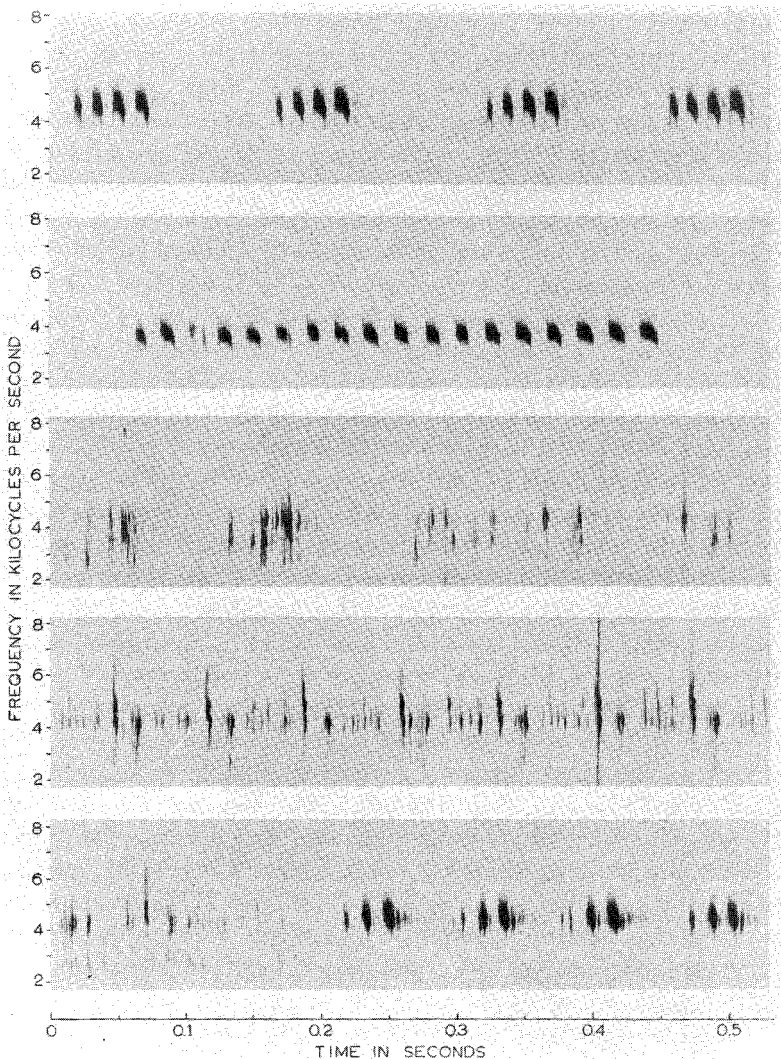suggest the following possibilities:

Fig. 16. Acoustic repertoire of *Gryllus campestris. Top to bottom:* calling,
fighting, first and second transitions to courtship, courtship, courtship interruption.

Brain-stimulated "calling" obtained heretofore is not calling at all but the first transition to either courtship or aggression, subsequent direction of modification in the sound depending apparently (in normal behavior) upon subsequent events. This "softened calling" or "transition 1" sound (Figs. 16 to 17) occurs generally when the calling (or silent) cricket is touched on the antennae. Calling, on
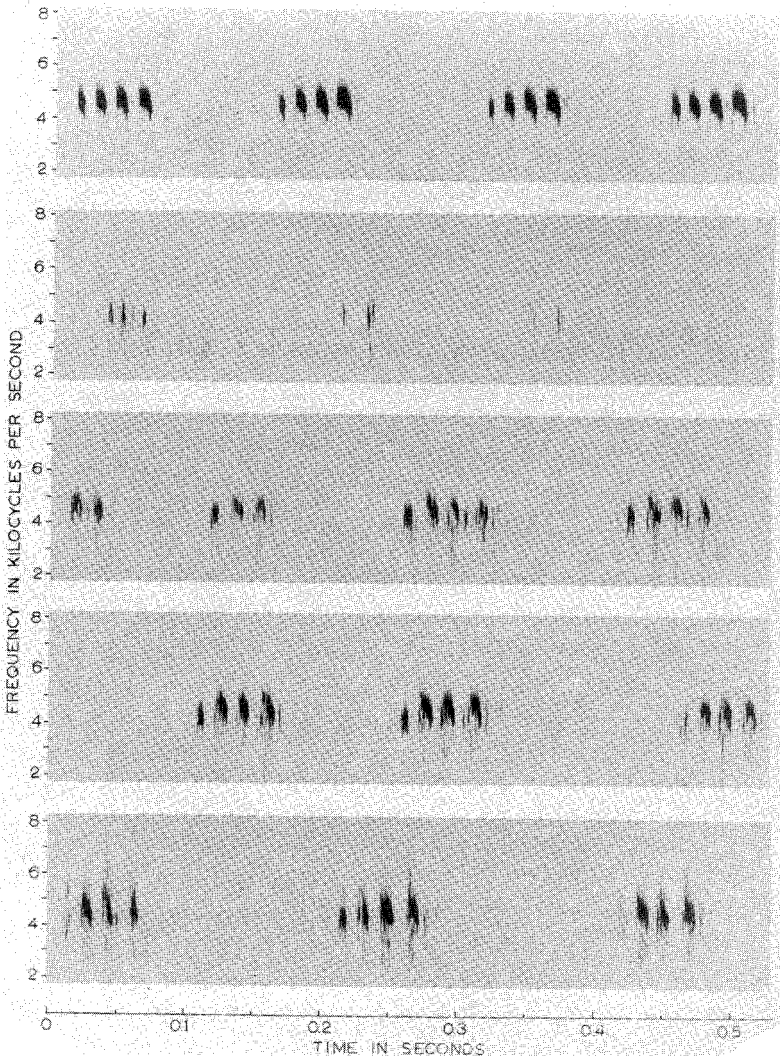

FIG. 17. Audiospectrographs of normal calling of *G. campestris* (top only) and brain-stimulated "calling" (lower four) (interpreted here as first transition to courtship, normally occurring when the male's antennae touch the female). (Recordings furnished by Franz Hüber.)

the other hand, occurs normally when the cricket is alone and to all indications cannot occur at all when there is appreciable antennal (or cercal) stimulation. Recently, Hüber (1965) has described the sounds in Fig. 17 obtained by brain stimulation as belonging to the "courtship" sphere, but this is confusing, as they are not "full" courtship and in fact contain neither of the two kinds of pulses characteristic of courtship. (Further, it brings up the question of what is meant by
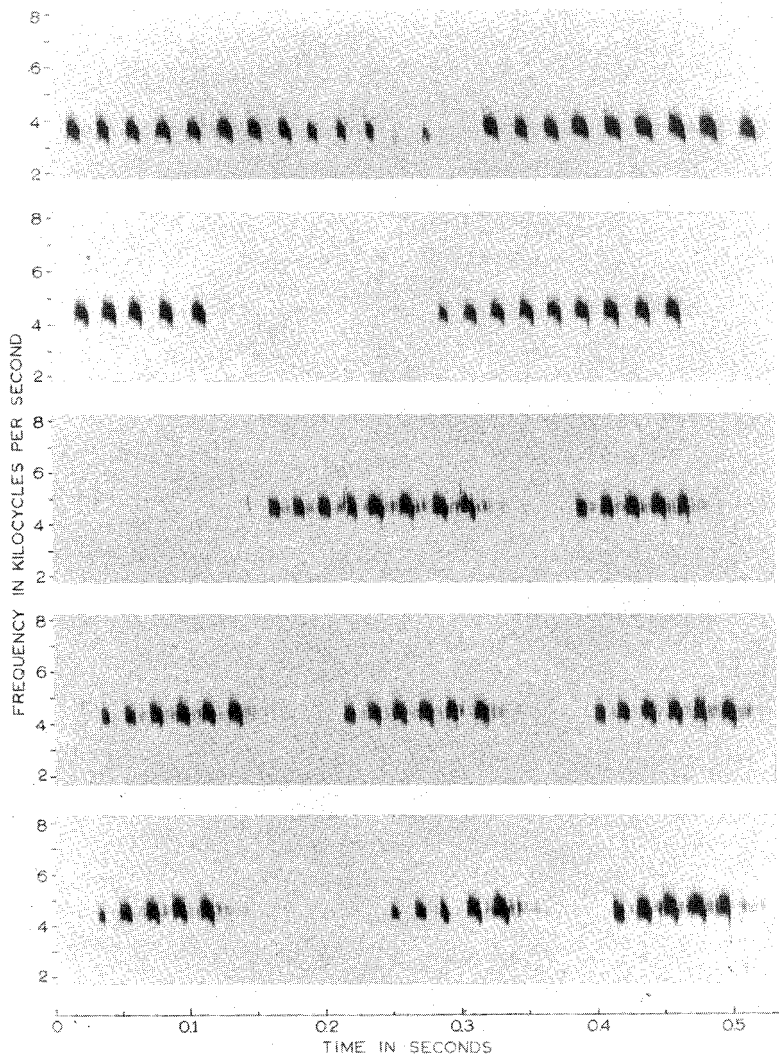

FIG. 18. Audiospectrographs of normal aggressive stridulation of *G. campestris* (upper two) and brain-stimulated aggression (lower three) (note more consistent chirp lengths). (Recordings furnished by Franz Hüber.)

"calling" in Hüber's discussions of sounds elicited by brain stimulation.) The structural difference between calling stridulation and first transition to courtship is subtle, and not apparent on oscillographs, but because it is the same difference that in normal crickets is referable directly to a change in external stimuli, it cannot be dismissed as trivial in the contexts in which it is being discussed by neurophysiologists.

The aggressive sounds obtained by Hüber by brain stimulation are more regular in length than normal aggressive chirps and are generally shorter, suggesting that sensory input, probably acoustic and tactual, is more or less directly involved in determining the length of aggressive chirps (Figs. 16 and 18).

Like "transition" sounds, aggressive chirps are produced when the antennae are stimulated (Alexander, 1961), so both of the sounds that Hüber obtained by brain stimulation (excluding preflight wing-whirring, which I think is the "atypical sound" he elicited by stimulation of the central body), seem to be associated with antennal stimulation, one with mild or brief stimulation, the other with violent stimulation. Further, Hüber's additional observation—cessation of calling upon brain stimulation—is another effect of antennal stimulation, for a male literally cannot call when his antennae are being strongly stimulated.

The parts of the brain Hüber stimulated, the mushroom bodies, receive fibers from the antennal lobes and, presumably, input from the antennae. The stimulation points eliciting aggressive stridulation, although not easily separated geographically as a group from those eliciting first transition to courtship, are generally somewhat peripheral to the latter. Since those eliciting aggressive stridulation are associated with effects of violent antennal stimulation and the others with effects of mild antennal stimulation, it seems at least possible that variations in the sounds elicited reflected variations in the size of the region stimulated that are related to normal variations in the intensity (and perhaps duration) of antennal stimulation.

The diagram in Fig. 19, particularly the structural nature of courtship-interruption sounds, brings up the question whether antennal input may also be necessary for both pattern elements of courtship stridulation; to my knowledge this possibility has not been tested. The courtship-interruption sound, produced when cercal stimulation stops, is reminiscent of antennal-stimulated sounds. The antennae are quite active during courtship, whipping backward across the male's body and touching the female (Alexander, 1961). Perhaps the full courtship rhythm depends upon high levels of both antennal and cercal input, while various transitional sounds are produced by fluctuations of input intensity between the two organs.
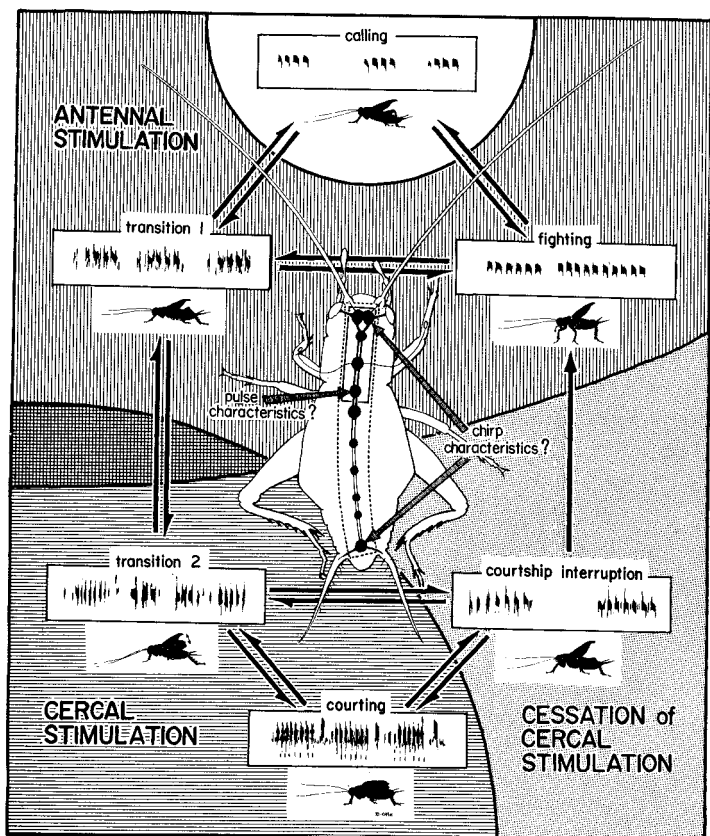
Fig. 19. Some of the transitional stages among sounds in the repertoires of the five field crickets studied neurophysiologically, their relationship to antennal and cercal stimulation, and some aspects of the known and suspected significance of various parts of the central nervous system in determining the nature of the components and patterns of the various sounds. Sound patterns are drawn from audiospectrographs of *Gryllus veletis* repertoire (Alexander, 1957). The solid rectangle inside the cricket encloses the parts of the CNS that Hüber's work has suggested are necessary for normal pulse and chirp characteristics in calling and fighting; dotted line encloses the parts evidently necessary for normal courtship singing. Although only the brain has been mentioned as a probable site for the chirp pacemaker, the prothoracic ganglion seems also a likely candidate, particularly because of the role of auditory stimulation in adjusting chirp intervals.

It is not surprising, in retrospect, that (1) neither sensory input nor proprioceptive feedback can alter certain aspects of the stridulatory patterns of crickets or that (2) the structures responsible for the pattern are located in the CNS and reflect genetic differences more or less directly in their functional variations. At this point the most interesting questions concerning neurophysiological mechanisms in cricket strid-

ulation seem to involve these postulated acoustic pacemakers: what are they, where are they, how many are there, how do they work, how are genetic differences translated into pacemaker differences, and how do they differ among species with different song patterns?

In 1950, Konrad Lorenz published a paper in which he described for the first time in English a now famous (or notorious) "hydraulic" (or "water closet") model for instinctive acts in animal behavior. The basic components of this model can be described by quoting its best-known critic, Daniel Lehrman (1953, pp. 338–339):

> To Lorenz, *the* instinctive act is a rigidly stereotyped innate movement or movement pattern, based on the activity of a specific coordinating center in the central nervous system. In this coordinating center, there is a continuous accumulation of excitation or energy specific for the act. When the animal comes into the appropriate external situation for the performance of the act, stimuli provided by that situation release the energy, the instinctive act is performed, and some or all of the excitation is used up. The center specific for the act thus is able to coordinate the instinctive act completely independently of the receptors, so that once the act is released (i.e., elicited) its performance occurs in complete form, coordinated by impulses from the center and without any chain-reflex character. The function of the stimulus is to release or elicit the act. Once released, the act no longer depends for its form on anything outside the central nervous system. When the animal happens *not* to be in the appropriate stimulus-situation, this reaction-specific energy is presumed to be accumulated, or dammed up. Also, the greater the amount of reaction-specific energy which has accumulated, the more easily may the act be elicited and the more complete will be its form when elicited.
>
> This picture is regarded by Lorenz as a representation of the neurophysiological basis of the above-described functional characteristics of the instinctive act. In particular, accumulation of energy in a neural center capable of determining the form and order of performance of the various movements of the act, independently of the receptors (except for a trigger-like elicitation), is postulated to explain the reaction-specific exhaustibility (using up of the specific energy), the presumed independence of the form of the act from concurrent external stimulation (reaction-specificity of the energy), and the lowering of the threshold during a non-exercise interval (i.e., when an accumulation of reaction-specific excitation is presumed to occur).

Reviewing the evidence presented above, we can state the following things about cricket stridulations:

1. All of the form of some of them, and some of the form of all of

them, is independent of external stimuli in the adult and is not appreciably or perhaps at all affected by proprioceptive feedback.

2. No environmental variations during development have yet been found to affect some of them, and evidence of close correlation between genetic and phenotypic variation has been found through hybridization. Their development is as rigidly canalized as that of any phenotypic character examined in these animals; moreover, there are reasons for believing that selection has favored the most rigid sort of canalization.

3. The precise portions of the patterns involved above depend for their nature upon postulated "pacemakers"—either single neurons or small groups of neurons—located in the mesothoracic ganglion (wing-stroke rates), possibly the brain (wing-hold or chirp intervals), and, in courtship stridulation, possibly the cercal ganglion. The postulated brain pacemaker, most interesting to us at this point, evidently fires continually at specific, temperature-dependent rates unless specifically inhibited. Only light–dark cycles, contact with other crickets, extreme temperatures, and disturbances are known to affect the calling cycles of males with spermatophores, and the effect in all four cases is evidently inhibitory. The only stimulative effects which might be suggested are (1) stridulation of other males—known to be stimulative (Alexander, 1961) and (2) the effect of the presence or absence of a spermatophore in the spermatophore pouch (Hüber, 1955). But crickets call without acoustic stimuli, and undisturbed crickets with spermatophores do not call continuously; the latter effect is not specifically known to be stimulative rather than inhibitory.

4. When a male is inhibited from calling for long periods, the specificity and intensity of stimuli necessary to elicit stridulation are greatly reduced, so that, sometimes, almost any kind of external stimulation, such as blowing lightly on the body, jarring the substrate lightly, or touching the antennae or cerci, is sufficient to cause aggressive or courtship stridulation. Likewise, calling, once started, sometimes can be prevented in such males only by gross and continuing disturbance. The calling song has long been termed the "spontaneous song" because its production is, at times, independent of known stimuli; this deficiency in our knowledge still exists. When certain presumably inhibitory centers in the brain are removed, a male cricket calls until a state of "complete exhaustion" (Hüber, 1962).

I can think of no significant way that cricket stridulation deviates from the criteria of Lorenz's original "hydraulic" model, constructed in a time of almost complete ignorance of CNS function and apparently largely discarded now as a useful construct, perhaps even by Lorenz himself. The similarity is certainly close enough to justify the

model and its use, even now, as a base line in the search for extremes and kinds of resistance to environmental variations among behavior patterns, whether essentially complete "units" of behavior in an arthropod or obscure fractions of behavioral responses in higher vertebrates. This is not a dichotomous view in regard to the developmental origins of all behavior patterns taken collectively, but it is dichotomous in terms of directions of selection, and thus in terms of the relationship between developmental origins of specific behavioral units, even though they may be parts of what is commonly described as a single behavior pattern.

The data given here not only prove that behavior essentially fitting Lorenz's model does exist, they explain its biological significance and, to a significant degree, they describe its neurophysiological, developmental, and hereditary correlates. Perhaps, whenever complex behavioral units have been keyed to pacemakers or hierarchies of pacemakers made up of single neurons or small groups of neurons, fulfillment of many features of Lorenz's model may be expected. Likewise, when selection is favoring behavior with the relationship to developmental and hereditary variations that occurs in cricket stridulations, evolution of pacemaker controls of the above sorts may be expected.

ADDENDUM

Since submission of this manuscript, M. Konishi (1966) has clarified several issues discussed here (the attributes of instinct, *Behaviour*, 27:316–328). He notes that we have acted, in behavioral study, as though the formula is always true that stereotypy = species specificity = inheritance = central coordination = spontaneity = self-differentiation. These things are not necessarily correlated and, as with learning, what has been called "instinctive behavior" is not a unitary phenomenon.

Also, D. M. Wilson (1967) has summarized the evidence for endogenous ganglionic oscillator functions in the patterned locomotory movements of insects and discussed the general significance of the findings (An approach to the problem of control of rhythmic behavior, In: Wiersma, C. A. G., *Invertebrate Nervous Systems,* Chicago, Univ. Chicago Press, pp. 213–229). The systems he discusses closely resemble that underlying cricket stridulation, and in the case of locust flight many elements involved are homologous with those found in the cricket stridulatory apparatus.

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