ACOUSTICAL COMMUNICATION IN ARTHROPODS

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Prior to the early 1950's, the study of arthropod acoustical behavior had been in a relatively stable state for a long time. Although hundreds of papers had been published on sound production and reception in insects, they had dealt chiefly with the morphology and physiology of devices that were either known or suspected to produce or respond to sounds [see bibliography (55)]. Only a few critical experiments on acoustical behavior had been performed (66, 68, 96, 113, 128–130). An abundance of review articles and books (13, 14, 37, 49, 50, 65, 111, 112, 123, 125, 131, 142) had failed to bring about any sustained growth of interest comparable to that enjoyed more recently by the field.

The accelerating development of electronic recording and analyzing equipment following World War II ushered in a new era, attracting a large number of workers into many aspects of the field of animal communication. In the course of 10 or 15 years, several hundred papers were published on arthropod acoustics, including five books (24, 51, 76, 85, 150) and an impressive array of review articles (1, 3, 6–8, 43–45, 54, 77, 124 and others). The recent volume on acoustical behavior of animals edited by Busnel (25) devotes 285 pages to articles dealing solely with arthropods by six different authors, and insects are prominently discussed in several of the other chapters. Nearly 500 genera of arthropods are mentioned, including representatives of 15 orders of insects.

The great preponderance of this recent work, inspired by the availability of new equipment and techniques, has involved descriptions and comparisons of the physical structure of the sounds themselves and of the ranges of responsiveness of auditory organs. Relatively little direct study of the communicative significance of the various signals has been carried out, though probably more than has been accomplished for any other animal group.

It seems clear that we are now on the threshold of still another era in the study of arthropod acoustics. The flurry of interest that generates whenever any new kind of biological information becomes available has largely faded. In some fields, such as systematics, applications have become well established and are incorporated into the methodologies of those active in the field (2, 5, 10, 146, 155, 156, 158). In other areas, such as insect control, there have been few or no encouraging developments (17, 56–58, 77, 89). Many of the workers who stepped into this field with the advent of new methods and equipment have stepped out again, and review articles seem to be proliferating faster than the research papers necessary for their sustenance. In short, the band-

1 The survey of the literature pertaining to this review was concluded in May 1966.
wagon of the late 1950's has disappeared, and we are faced with the question
of what to do ultimately with information derived from the study of arthropod acoustical behavior which, in turn, determines how hard we are going
to work at studying it, and who is going to do the studying.

Part of the answer to these questions derives from what has been happen­ing in related fields. The rise of interest in arthropod acoustical behavior has
coincided with an intensifying of concern among zoologists with the whole
field of animal behavior—sparked by the extensive contributions of Euro­
pean ethology, the examples of investigators such as Karl von Frisch and
his students in their work on honey bee biology, and a growing realiza­tion of
the importance of behavioral information to the kinds of syntheses with
which zoology is increasingly discovering itself to be concerned.

One might say that, together, the various specialized fields of animal
behavior—of which arthropod acoustics is one—have, once again, produced
an embryo. If we can agree that this one is not a monster which ought to be
aborted as quickly as possible, then our problem is how best to nourish it
and guide its development. The study of animal behavior has had trouble
before because this problem was not solved. In fact, only one of the many
such embryos that zoology has produced has survived; this is psychology,
whose foster parents, medicine and philosophy, have provided it with an
adequate livelihood and considerable security, though in large part well out­
side the zoological family.

Perhaps the problems involved in behavioral study by zoologists will be
solved this time before it is too late. I think the nucleus of an answer lies
in the early efforts of such biologists as William Morton Wheeler and Konrad
Lorenz to focus attention on the role of natural selection in shaping behavior.
Only when biological attributes are examined under the continuing realiza­tion that they are, in one way or another, always a result of long, compli­
cated sequences of selective action, can we be confident that the most appro­
priate routes have been taken toward their understanding—whether in terms
of physiological mechanisms, ontogeny, or heredity—and their eventual
incorporation into reconstructive and predictive frameworks relative to the
process of organic evolution. But there is another requirement, and this is
that we must also acknowledge finally that behavior has always played a
central role—perhaps the central role—in mediating the effects of natural
selection upon animals. Simpson (141) has said it this way: "Behavior is
subject to particularly strong selection, and it is probably farthest removed
from the genes. . . . As a rule, with exceptions, the effect [of selection] be­
comes more, not less, diffuse, and less, not more, direct as the level of the
gene is approached."

Specialized acoustical behavior, unlike specializations associated with
chemical and visual input or output, is always a communicative phenomenon
in all kinds of animals. It does not matter whether the signals are functional
intraspecifically or interspecifically, or even if they are used solely by the
individual producing them, as in echo-location; whether they are transmitted
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aerially, aquatically, through solid substrate (with air-transmitted portions that we hear only incidental to the signals themselves), or even only through direct bodily contact. To be examined in terms of selective action they must be studied as communicative units. Communicative functions, in turn, cannot be hypothesized effectively without comprehensive knowledge of the species involved: their life histories, ecology, and systematic positions—most particularly, their hour-by-hour, day-by-day, season-by-season activities.

In light of these considerations, I believe that the biggest problems and the most important contributions in the study of arthropod acoustics lie in analyzing it directly as a communicative phenomenon on a much more extensive scale than has been the rule, and in developing the available information in such a way as to make it more useful in a comparative sense, particularly with regard to the broader fields of animal communication and animal behavior in general. The present review has been written with this theme in mind; its organization has been influenced by a few recent papers dealing with the general aspects of animal communication (79, 115–117, 167).

SOME GENERAL CONSIDERATIONS

Communication can be defined as the transfer of information from one organism to another, detectable to an outsider only through the appearance of an observable response in the receiving individual. In its more complex forms it may become reciprocal in nature, and it may involve anticipation, delayed response, and other special complexities, depending upon the kind of system and the animal involved. But the near-universality of phenomena of this nature among animals, the continuity from simple expressions of communication to complex ones, and the certainty that all complex systems have evolved from simple ones, militate against restricting the idea of communication, as many authors have done, to its more complex expressions and thereby to certain systems occurring only in humans or the higher vertebrates.

Information can be transferred between organisms by means of chemicals (olfaction, taste), light waves (vision), sound waves (hearing), substrate vibrations, direct contact, or even by temperature and (at least theoretically) humidity changes. Callahan (33–35) even speculates that moths communicate by “high-frequency microwave electromagnetic radiation.”

Communication can be either intraspecific or interspecific [sometimes the latter has been termed “extraspecific”—Leston (98)], though it is more apt to be complex and multifaceted in intraspecific contexts, for the obvious reason that members of the same species are more likely to possess a variety of mutually significant communicative contexts. For example, with a few exceptions (such as alarm calls in some birds and mammals), only conspecific individuals interact in interchangeable roles.

As Wilson & Bossert (167) propose and exemplify for chemical signals, response to a communicative signal may be immediate and direct (releaser
effect) or delayed and indirect, through some kind of physiological adjustment (primer effect). Most communicative responses studied so far are of a releaser nature, and except for mammals primer effects in acoustical systems have been demonstrated only in birds. Included in this category are such phenomena as the delayed effects of exposure to adult songs during critical periods in the lives of some birds (118, 147); production, by one member of a pair, of phrases previously uttered only by the other member, following removal of the latter (148); and changes in the nesting and molting cycle of budgerigars resulting from the addition or deletion of budgerigar sounds from the environment (52).

With regard to nonacoustical kinds of communication, primer effects (changes in morphology, physiology, and behavior associated with “phase” differences) have been demonstrated for tactual, chemical, and visual signals in migratory locusts (47, 92, 93, 109), and tactual and visual signals in field crickets (69, 100). Examples given by Wilson & Bossert for chemical signals include the inhibiting of worker ovary development by queen substances in social insects such as ants (18), termites (110), honey bees (32), and the timing of female reproductive cycles by the odor of male urine in mice (121).

The number and kind of communicative signals in the repertoire of an animal species depend upon the complexity of its life activities (the number of contexts in which signals can be used), the number and kind of communicative systems it employs (each with its own peculiar limitations and potentialities), and the number and kind of potentially confusing signals produced by other species within its habitat. Selective action on communicative systems ought to: (a) maximize the effective range and directionality of signals; (b) increase the number of useful contexts for any given kind of communicative system; and (c) either minimize or maximize aspects of signal similarities within and between species repertoires, depending on the context (for examples, compare the functions of reproductive isolation and mimicry). These changes increase the amount of information transferred per unit time, per situation, and per communicative system.

CLASSIFICATION OF COMMUNICATIVE FUNCTIONS

Various schemes of classification have been proposed for the purpose of generalizing the contexts of animal communication. Dethier et al. (39), referring to the kind of action involved in the response and moving from the general to the specific, provided a logically exhaustive list of six possible functions of communicative signals: 1. locomotor stimulants, 2. locomotor depressants, 3. attractants, 4. repellents, 5. stimulants of specific acts, and 6. deterrents of specific acts. Wilson & Bossert (167) described six functional contexts for chemical-releasing stimuli which correspond to the above classification as follows: 1. trail marking (attractant), 2. sexual stimulation (stimulation of a specific act), 3. aggregation (attractant), 4. nonterritorial dispersal (locomotor stimulant), 5. territory and home range marking (repel-
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lent), and 6. alarm (stimulant of specific act, attractant, repellent, and locomotor stimulant, under different conditions of intensity and other accompanying stimuli).

Alexander (6), in classifying acoustical signals in crickets, referred first to the kinds of individuals between which the signals passed. To make such a classification reasonably complete, even for arthropod communication and including provision for signals passing both ways between different kinds of individuals, a rather large number of categories would be necessary: 1. male—female, 2. male—male, 3. parent—offspring, 4. juvenile—juvenile, 5. species—species, and (for social insects), 6. reproductive—sterile caste, 7. juvenile—sterile caste, 8. sterile caste—sterile caste. The list would have to be further complicated by, among other things, provision for distinctive signalling involving different kinds of sterile castes and different juvenile stages. For crickets, Alexander described only six acoustical signals, all in the first three categories: (a) calling (pair-forming) 1, 2; (b) aggressive 1, 2; (c) courtship 1, 2?; (d) courtship interruption (pair-reforming?) 1, 2; (e) postcopulatory (pair-maintaining) 1, 2; (f) “recognition” 1?, 2?, 3?. An unpublished observation by Daniel Otte (personal communication) on stridulation by a South African *Brachytrupes* species (Brachytrupinae) as it was being dug out and seized in the bottom of its burrow, indicates that a disturbance sound (g), presumably in category 5 above, should be added, giving the probability of seven functional kinds of signals in the collective acoustical repertoir of all crickets.

Three factors complicate any attempt to generalize and classify communicative functions:

1. The functions of signals, measurable responses to them, and their structural nature may “blend” imperceptibly or vary independently between obvious functional foci.

2. Intensity, context, physiological condition of potential respondents, and, in some kinds of animals, individual recognition or prior experience, can change effects of signals.

3. Any signal can have an effect on members of other species, either without selective significance or in a way that will (at least initially) have a principal selective significance only with regard to the responding species (for example, predators may be attracted by the sexual signals of prey species).

To illustrate some of these complications, there is evidence that under different circumstances the calling sound of male crickets can (a) attract predators (157); (b) attract females (3, 129, 154); (c) act as a locomotor depressant (at high intensities) for females; (d) cause aggressive chirping and other aggressive actions; (e) stimulate calling by other males; (f) inhibit calling by other males; and (g) cause other males to move away (3, 4). Every one of Dethier’s six signal functions is included in this list.

In effect, it almost seems that one can devise an appropriate classification of communicative functions only when one is able to devise an appropriate classification of all functions in animal behavior. It was evidently for this
reason that Wilson & Bossert (167) found it necessary to restrict their discussion of selective action on chemical communicative systems to "several specific cases within a narrowly defined function." On the other hand, studies of animal communication have, in many cases, led the way in the establishment of significant generalizations in behavioral work, and the obvious and striking parallels among signalling functions in insect communication indicate that an appropriate system of classification would offer more than mere nomenclatural convenience. Thus, it appears that all of the known and suspected functions of arthropod acoustical signals can be arranged in nine categories, using nomenclature that is at least roughly comparable to that used by the investigators studying them in different kinds of arthropods:

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.
5. Courtship interruption (pair-reforming?) signals.
6. Copulatory (insemination-facilitating and pair-maintaining) signals.
7. Post-copulatory or intercopulatory (pair-maintaining) signals.
8. Recognition (pair- and family-maintaining) signals (limited to sub-social and social species).
9. Food and nest site directives (limited to social species).

This classification is not comprehensive, even for arthropod communicative systems. For example, a context not included in a clear fashion involves signals resulting in the transfer or exchange of food, chemicals, or other materials, most often in social species, and frequently referred to as "trophalaxis" (138, 165). Another example worthy of mention is the finding by Lloyd (107) that predaceous females in the firefly genus Photuris "attract and devour males of the genus Photinus by mimicking the flash-responses of Photinus females."

GLOSSARY OF TERMS FOR DESCRIBING ARTHROPOD ACOUSTICAL SIGNALS

Two systems of nomenclature for arthropod acoustical signals have been proposed (20, 36), but neither has been widely accepted or used; Broughton's terminology (20) was not even used by many of the other authors writing in the same book. There seem to be two reasons for the failure of these efforts. First, each has been unwieldy and rigid, and has attempted to assign one-word labels to signals that are too complicated and unusual for any significant information to be transferred without detailed description. Second, each has departed so violently from common everyday usage as to cause awkward, strained efforts by investigators attempting to use the terms, and to make the learning of an entire new vocabulary necessary for every reader of a paper on insect acoustical behavior. A useful glossary must be short, natural, and open to the addition of terms describing kinds of signals not yet encountered. It
must also take into account all of the different reasons for naming signals or ways of naming them—the known or presumed function of the signals, the nature of the movements or the device involved in making the signal, the onomatopoetic effect of the sound produced, and the physical nature of the sound. Onomatopoetic terms ought to be used in ways that conform closely to their dictionary definitions. Physical descriptions ought to use terms in conformity with their usage by acousticians, with the exception that acoustical signals of animals involve some combinations and kinds of units for which the acousticians have no adequate names, or for which the terms used by acousticians can be employed only through some slight stretching of their original meanings. Labels depending upon knowledge of function should be used when possible because of their high communicative value, but not before some reasonable basis for their introduction is established. Labels relating to movements of the sound-producing apparatus are least controversial, and can be applied with relatively little difficulty.

The following list of terms, in the preparation of which I have been helped by Dr. Thomas J. Walker of the University of Florida and Dr. Thomas E. Moore of the University of Michigan, seems in large part to meet the above requirements:

**Frequency**: Cycles per second (not too different in meaning from the subjective word "pitch" when simple sounds within the sonic range are being considered). Any other repetitive units should be described in terms of rates (pulse rate, phrase rate, chirp rate, trill rate, wingstroke rate, tooth-strike rate, etc.). The principal or dominant frequency is the physically most intense one (not necessarily the loudest to human ears); a pure frequency (only theoretically possible) is a single one; the fundamental frequency is usually the lowest one. (Multiples in terms of cycles per second are termed harmonics. Any additional frequencies higher or lower than the fundamental can be termed overtones or undertones, respectively; it is usually easier to avoid this term "fundamental" frequency than it is to be certain you're using it accurately. The main problem is that passing a sound through any kind of analyzing or recording device may introduce into it new harmonics or change the relative intensities of those originally present). Frequencies can be down-slurred or up-slurred (changed in a gradual fashion), modulated (changed regularly) in either intensity or frequency (the latter by regularly changing the frequency up and down), or pulsed (broken into separated units). If a frequency is above the (maximal) human hearing range (about 20,000 cycles per second), it is termed supersonic or ultrasonic; if it is below the (minimal) human range (about 50 cycles per second), it is subsonic.

**Pulse** (example: a very brief human whistle): a physically unitary or homogeneous sound—in the most restricted sense, a brief succession of sine waves (which, among insect sounds, is approached principally in cricket stridulations and wingbeat sounds). This term has been used by most bi-acousticians in a slightly less restricted sense than the physical acousti-
cially dominated by a single or multiple pulses, most often strongly or "zzzzzzeee-zee-zee": any succession of pulses, most often strongly dominated by a single or a few frequencies (having a definite tone if it is
sonic), which lasts too long to be called a chirp and is too uniform and rapidly delivered to be called a phrase. Unless a trill extends indefinitely (which should be specified), length and uniformity of both trills and their intervals (as with chirp and phrase sequences) ought to be specified. A ringing telephone is a short trill, but on a party line there will be groupings of variable numbers of trills of the same or different lengths. The pulses in a trill need not all be of the same frequency or length or delivered at the same rate. The label complex trill can be used, but, depending upon the kind and degree of complexity, each such sound will probably have to be described. Thus, it wouldn’t be very communicative to refer to a whistled rendition of Yankee Doodle merely as a “complex trill.” Broughton (20), using strict musical definitions, would like to restrict this term to sequences in which two different tones are alternated and use “tremolo” for successions of like tones. While I cannot disagree with his definitions, this would practically eliminate the quite widely used and understood term “trill;” I doubt that this is possible, or important to try to do.

**Buzz** (example: a telephone buzzer signal): sounds that are patterned like trills, but because they have more or less wide frequency spectra are much different in quality (lack tone), and don’t bring to mind the word “trill” in the sense of cricket sounds, or whistles. Phone buzzer signals are usually short buzzes, or perhaps a broken buzz, while most electric alarm clocks produce continuous buzzes (or trills).

**Group:** This simple term is so useful, particularly as a descriptive modifier, that it deserves special mention. All of the rhythm units described above are either grouped or ungrouped in different insect sounds. An ungrouped series or succession of pulses would be a succession of chirps, phrases, or short trills. A group of three pulses may be called a chirp or a phrase, depending upon the speed of delivery and uniformity of length of intervals and pulses; a group of 50 pulses would be a short trill. There are secondary and tertiary grouping of all of the above rhythm units in the most complex insect sounds.

**Sentence:** Broughton (20) suggests the use of this word, more or less in the dictionary sense of “a complete musical expression” to refer to the long, sometimes complicated units of sound made by several kinds of insects, for example, *Amblycorypha uhleri* Stål (3). I have not previously used the term, but if its meaning becomes widely understood it may be a good addition to the bioacoustical vocabulary.

**Phoneme** (from linguistics): Structural units in communicative sounds which are too small to have meaning (transmit information; cause responses) by themselves (analogous to letters in a written language and individual sounds in a spoken language).

**Morpheme** (from linguistics): The smallest structural units which have meaning (analogous to words in written and spoken language). Phoneme and morpheme are terms used by the linguists specifically for human language. Hockett (79) would prefer that the more general terms, “ceneme” and
"plereme," be used for "nonlinguistic" signals, by which designation he would include nonvocal signals of all sorts, such as arthropod acoustical signals and all tactual, chemical, and visual signals. It seems to me that the break might better be made between acoustical and nonacoustical kinds of signals.

Any sound too complex to be described by one or more of the above terms might as well be described in detail. Examples are sounds involving gradual or sequential changes in rates of delivery of rhythm units, or different kinds of groupings following one another in some regular succession. The usefulness of any kind of generalized terminology diminishes as the involved patterns increase in complexity and individuality.

A point that perhaps should be made here concerns the tendency of some investigators to designate as "complex," sounds that are essentially without rhythm or tone and within which, therefore, the information-bearing components are difficult to identify. As mere physical entities, such sounds may indeed be "complex" (compared to, say, a three-pulse house cricket chirp), but as acoustical signals, they are much more likely to be merely rudimentary and simple.

**DEMONSTRATIONS OF COMMUNICATIVE FUNCTIONS**

**General**

Stridulatory organs and other devices known to produce sound or suspected of producing it have been described in thousands of arthropods, including practically all of the insect orders (7, 8, 43, 55, 95). Likewise, vibration-sensitive devices believed to be capable of responding to substrate- or contact-transmitted vibrations are almost universal among insects (38, 55, 139). Recent experiments suggest that if sounds are produced at unnaturally high intensities, almost any insect can be made to respond—at least in a "phonokinetic" or nonoriented, spasmodic fashion (22, 23); by this, the necessity of giving some indication of intensity in all experimental studies is underscored.

Clear demonstrations of response to air-transmitted sounds resembling some known stimulus in the arthropod’s environment have so far been restricted to a few orders of insects: Orthoptera (26–31, 66–68, 122, 128–130, 154), Homoptera (9, 144, 145), Lepidoptera (7, 132–135), Coleoptera (114), and Diptera (89, 136, 168). Demonstrations of response to air-transmitted sounds produced by conspecific individuals are still restricted to Ensifera and Caelifera (Orthoptera), Auchenorrhyncha (Homoptera), and Culicidae (above references). Specialized responses to substrate-transmitted sounds (or vibrations) produced by conspecific individuals have been demonstrated in bees (105, 106, 161, 162), termites (80), and crabs (137).

In this and following accounts, investigations may be known to readers which have been omitted, yet seem to illustrate phenomena being discussed. I have excluded numerous publications often included in similar discussions
because I have restricted examples to what seem to me to be actual demonstrations of function. Doubtful papers excluded fall mostly into three categories: (a) anecdotal descriptions of behavior without specification of adequate controls or sufficient repetitions of improbable sequences to lend credibility; (b) experiments in which sound intensities were not indicated, so that phonokinetic effects, for example, could be involved; or (c) experiments in which substrate transmission could not be ruled out and is not unlikely on the basis of the animal involved and the experimental set-up described. It is most difficult to survey the literature so exhaustively that flatly exclusive statements can be made, and some errors of omission may occur. I feel, however, that the effects of a few such errors are outweighed by the value of the kind of straightforward generalizations that inclusion of doubtful results often precludes.

INTERSPECIFIC INTERACTIONS

Responses to substrate-transmitted vibrations have been extensively analyzed in spiders (101, 152) in connection with methods of detection of prey struggling in the web, and (less extensively), in ant lions in connection with detection of prey struggling on the sloping walls of the larval burrows (127). Responses to air-transmitted sounds produced by other species of animals in a natural situation have been demonstrated only in certain Lepidoptera, in connection with the strong likelihood that flying moths avoid predatory bats by responding to their echo-location signals (132–135, 149).

In spite of considerable speculation, summarized and discussed by Walker (157), there is only one demonstration of a vertebrate predator locating arthropod prey by its noise. Walker observed two domestic cats apparently locating crickets and katydids by their sounds and demonstrated that one of the cats was attracted to the electronically reproduced sound of a katydid from 30 feet away.

One claim has been made for acoustical mimicry in an arthropod (97). The authors believe that the disturbance stridulations of burying beetles (Silphidae: Necrophorus spp.) have been selected toward resemblance to the buzzing of disturbed bumble bees, and that the leg-waving behavior and froth-covered appearance of a disturbed, stridulating beetle lying on its back furthers the resemblance. The report is detailed and the suggestion not unreasonable, but in the absence of experimental tests with animals that might have been responsible for such selection, no conclusions can be reached. Many of the described facets of resemblance, including the general nature of the sounds of bumble bee and beetle compared, are by no means restricted to these two kinds of arthropods.

The report by Broughton (21) of song “learning” in Tettigoniidae, based on two chirps supposedly produced by an individual of Platycleis sabulosa and resembling a sound he otherwise had heard only from P. affinis, can be mentioned here, since it, too, is the only such claim to be made for an arthropod in recent years. The only parallel seems to be the reports by several
investigators of inducing changes in the lengths of chirps made by males of the true katydid, *Pterophylla camellifolia*, by playing long chirps to them (3, 123, 140). In these cases, however, the same change occurs in natural situations and seems to be related physiologically to simple inhibitory and stimulative effects between neighboring katydids, and functionally to aggressive signalling and whatever effects accrue from long-continued alternation (see Phonoresponses and Aggregation below).

**Disturbance and Alarm Signals**

Sounds made by arthropods held in the hand, or disturbed in various manners such as by pinching, probing, or restraining, are known in almost every order of insects (3, 7, 8, 55, 76). This kind of response exists in one or more species in every major arthropod group suspected or known to have specialized sound production. In no case, however, has a function been demonstrated for the air-transmitted portions of stridulations or other noises made during disturbance, except, of course, that humans can hear such noises and often react to them. The sudden squawk of a seized cicada or katydid might cause one to drop it or allow it to escape; Leston & Pringle (99) state that “The sudden loud outbursts of a large reduviid when picked up by a trained observer often causes him to drop it. . . .” Except for the unproved possibility that similar reactions have been given by vertebrate predators in the past, however, such human responses do not afford much insight into the evolutionary processes leading to elaboration of disturbance sounds. I have witnessed the seizing of cicadas, both in mid-air and in trees, by several different species of birds, but I have not yet seen a cicada escape following its squawk when so seized. Cicada squawks may cause other cicadas to fly (3), but there is no clear evidence of this.

Howse (80) has reported the only detailed experimental investigations of the probable causes and effects of an arthropod disturbance or alarm sound in the termite, *Zootermopsis angusticollis* (Hagen). He found that the tapping noise reported from termite colonies is caused by soldiers striking their heads against both the roof and the floor of tunnels and by workers striking their heads against the roof, producing sounds with a frequency (in termite-infested wood) of around 1000 cycles per second in bursts of two to eight pulses delivered at rates equivalent to 24 per second at 20 to 21° C. These sounds are elicited by some kinds of stimuli that elicit so-called disturbance sounds in other arthropods—substrate vibration, sudden exposure to bright light, and puffs of air. Howse was able to obtain responses only by transmitting the sound through the substrate, and his findings indicate that termites change their responses to chemical, tactual, and gravitational stimuli when presented with substrate vibrations, that they often respond to a vibration by making one themselves, that they produce vibrations upon encountering other termites, and that they receive the vibrations through the tibial subgenual organs which are tuned somewhat to the frequency and pulse rate in their particular disturbance response.
Howse's papers offer an example of how to approach the problem of communicative function and selective significance of so-called disturbance "sounds" in arthropods. Interest in this subject is obviously great. More papers are published on stridulatory structures and sounds in arthropods with this general kind of behavior than on any other aspect of arthropod acoustical behavior, and more arthropods fall into this category of having only a disturbance sound of unknown function than into all other categories of acoustical behavior combined. Two general suggestions seem pertinent for investigators involved with these problems: (a) view the stimuli as possibly being elaborate tactual or vibratory communicative signals rather than as strictly rudimentary acoustical signals, and proceed as if the air-transmitted portions of the signals (the parts we hear) might be incidental; (b) expect the principal functions to be intraspecific and learn enough about the biology of the species involved to know what kinds of interactions, either at close range or during actual bodily contact, might be mediated by tactual or vibratory stimuli. Discovery of specific signals in courtship situations in various Coleoptera (11, 114, 151) and Hemiptera [see review by Leston & Pringle, (49)] previously known to produce noises only when disturbed, emphasizes the likelihood that several intraspecific functions exist. However, it should be emphasized that the study of some of these groups has yet to pass beyond the anecdotal stage in which our knowledge of orthopteran and homopteran acoustical behavior had largely remained until a short time ago.

PAIR FORMATION AND REPRODUCTIVE ISOLATION

The usual events of sexual behavior, in order, are pair formation, courtship, copulation (or better, insemination), and sometimes pair-maintenance and further inseminations; in some species, pairs are formed chiefly or only within previously formed aggregations of sexually responsive individuals. Aside from the influence of predators, selective action on these various events may be viewed as solely a matter of maximizing efficiency of the sequence within species—that is, decreasing the percentage of unmated individuals and the percentage of prematurely aborted, sexually significant encounters (the amount of wasted time and energy). But, for any species, the particular nature of individual units in the sequence may be explainable only in the context of reproductive isolation, in other words, only in relation to the nature of the same units in the behavior of other species living in the same area and sufficiently alike to be potentially confusing to the animals themselves. If two similar species live together long enough, it seems probable that events occurring early in the sexual sequence will eventually become sufficiently different that they will operate as the functional reproductive isolating mechanisms regardless of the nature of the original difference that made interbreeding or interaction between the species deleterious (5, 40, 46). Thus, differences in the manner of pair formation would prevent deleterious interaction between similar species more effectively (that is, involve less wastage of time and energy), than, say, courtship differences; courtship differences in
turn would be more efficient than mechanical barriers to copulation. As a result, selection ought to continue to promote divergence in pair-forming signals (or aggregating signals) even following the appearance of differences in the nature of other events occurring later in the sexual sequence; in contrast, diverging selection on later events would cease when early events became completely effective. This is why calling or pair-forming signals of any sort, in any kind of animal, are more than just another taxonomic character (5); they alone (as a definable group of characteristics) can be expected to distinguish all the species in any well-established situation. Such characteristics include not only aggregating or pair-forming chemical, visual, and acoustical signals, but the separation of adults of different species during breeding time by differences in daily or seasonal cycles, or by habitat differences. These are features of arthropod biology that cannot be ignored in any effort to distinguish the species in any group. In some animal groups, such as many birds, humans use the same things the animals evidently do to distinguish the species (plumage, song, eye and bill color); in most arthropods this is not true, and I must confess to a large amount of skepticism whenever any insect group is treated as if the species had been defined when pair-forming mechanisms have not yet been studied. Part of the lesson deriving from this theme involves the value of the "local fauna" beginning in the taxonomy of any group. Perhaps the closest parallels to acoustical signalling in this regard, and excellent recent examples, are the studies of Barber (15) and Lloyd (108) on fireflies.

**Calling Signals**

Function has been demonstrated more frequently for pair-forming or calling signals than for any other kind of insect acoustical signal. Most often, pair formation is accomplished by the simple attraction of the sexually responsive female to the signalling male. Such responses have been demonstrated in Gryllidae (3, 129, 154), Tettigoniidae (26-28, 42), and Cicadidae (9), and are likely in crabs of the genus *Uca* (137). In some insects, males are attracted to acoustical females; such a response has been demonstrated in Culicidae (136, 168) and Ceratopogonidae (41), and is possible in beetles (Trogidae) (11). In still other cases, there is movement by both males and females as a result of hearing the other's sound, and a series of phonoresponses as well. Such interactions have been demonstrated in Acridinae (29-31, 75, 85) and Tettigoniidae (12, 67, 143). Recently, Mampe & Neunzig (114) reported that males and females of the plum curculio, *Conotrachelus nenuphar*, are attracted to cages of stridulating individuals of the opposite sex, but not to cages containing silent individuals with their elytra removed or glued down.

Most of the evidence by which we can decipher how selective action has operated upon insect acoustical systems is still of an indirect nature. Not all such evidence, however, is completely unreliable or lamentably tenuous, as can be illustrated with the role of pair-forming acoustical signals in the effi-
iciency of reproductive isolation among sympatric, synchronic species. If a particular signal is chiefly responsible for pair formation in any group of species, then differences between signals of species living together would prevent wasted time and energy in deleterious interspecific interactions. This says nothing about why the interspecific interactions are deleterious—a question worth more attention than it has received in the light of our increasing awareness of the prevalence of the potential of closely related animal species both vertebrate and invertebrate, to produce viable hybrids on a wide scale (5, 19, 71, 72, 81)—and it says little about the manner in which such interspecific signal differences might arise. But it does give us a basis for further investigation. Thus, if insect acoustical signals are important in reproductive isolation, then we should expect first that species reproductively active in the same places at the same times would not have identical acoustical behavior. This expectation has proved justifiable. In spite of the fact that more than half of the 1000 or so species of Orthoptera and Homoptera in North America and Europe have been studied to some extent, no case of identical or confusingly similar acoustical behavior has been discovered between sympatric, synchronic species (3, 6, 24, 25, 49, 50). Second, we should expect that some recently diverged species that are still isolated either temporally or geographically would have identical or very similar sounds. Several such cases have been reported for insects (5); evidently, none has been reported for vertebrates. *Gryllus veletis* (Alexander and Bigelow) and *Gryllus pennsylvanicus* Burmeister, seasonally isolated sympatric field cricket species in North America, each have a wingstroke rate of 25 to 27 per second at 75°F, a mode number of four pulses in the calling chirp, variable, similar chirp rates, and the same frequencies (cycles per second) in their calling songs. *Gryllus campestris* Linnaeus in Europe, with a wingstroke rate of 27 to 28 per second, has an identical (or extremely similar) calling song in all other respects, even to the variable chirp rate (about 100 to 300 per min), the mode pulse number in the chirp (four), the range of from three to six pulses per chirp, and the frequency of the sound (about 4.5 kc per sec). These species have perhaps been isolated since the Oligocene period, *G. campestris* living almost alone in Europe, with no congeneric sympatric species except for an apparent slight overlap with *G. bimaculatus* De Geer near the Mediterranean (a detailed description of the geographic, seasonal, and ecological overlap between these two widely studied species has, to my knowledge, never been published). *G. bimaculatus* has a song that seems to be identical to that of *G. campestris* except for a pulse rate of 25 to 26 at 75°F. This difference is probably too slight to be effectively significant to the crickets, especially since the figures given here are based on recordings of only a few individuals. For instance, Walker (154) found that the pulse rate differences between the trills of *Oecanthus quadripunctatus* and *O. argentinus*—36.5 and 44.25 per second, respectively, at 74°F—could be eliminated by less than a 10°F difference in temperature. Such a shift would cause the song to attract females of the wrong species. The closest relative of *G. pennsylvanicus* and *G. veletis* in North
America is *G. firmus* Scudder, an Atlantic and Gulf Coast cricket, with a pulse rate of 17 to 18 per second at 75° F—almost surely a significant difference. *G. bermudensis* Caudell, found only on Bermuda, is undoubtedly derived from *G. firmus*, perhaps during the Pleistocene, and is allopatric with *G. firmus*. One individual recorded had a pulse rate of 14.0 per second at 75° F, probably not communicatively different (to the crickets) from the song of *G. firmus*.

Finally, we should expect that species which overlap would differ more in regard to acoustical behavior where they overlap than where they do not. Only two possible cases have been reported. Alexander (2) suggested that *Gryllus fultoni* (Alexander) may have developed a faster, more regular chirp in the northern part of its range. In that region it overlaps ecologically with two chirping species absent in the southern part of its range—*Gryllus veleiis* (Alexander and Bigelow) and *G. vernalis* Blatchley. Character displacement, it must be emphasized, is still a highly speculative possibility in this case. The change involved does represent a divergence from the song characteristics of these two species, and only a single trilling species overlaps ecologically and temporally with *G. fultoni* in the south where its chirp is less regular and more slowly delivered.

Walker (155) suggests a similar and probably more positive case in North American tree crickets. *Oecanthus fultoni* Walker shows geographic variation in chirp rate, western individuals that overlap with the similar and more slowly chirping species, *O. rileyi*, having a faster chirp rate. On the other hand, Thomas & Alexander (146) failed to locate evidence of character displacement in song among three meadow grasshoppers with distributions that provide an almost optimal model for this phenomenon—linear distributions with geographic and ecological overlap only at the two extreme ends of the distribution of each of three species.

Why are there so few cases of song identity among allopatric and allochronic species and so few cases of local divergence in regions of overlap between similar species? Thomas & Alexander suggest that the three meadow grasshoppers they studied may have diverged in this regard before acquiring their present extensive ranges; that is while living together in a restricted southern location near their present southern overlap. Pulse rates in the songs are almost as different as is possible—nearly multiples of one another. Another possibility is that song change, while seeming necessarily to be a relatively conservative evolutionary feature because of the communicative function (which requires that response capability change each time signal structure changes), nevertheless may occur between two species even while they are still allopatric or allochronic because of some confusing similarity of the song structure to the songs of other related or unrelated species in the same habitats. In a region such as North America, where 40 or 50 insect species may be stridulating simultaneously, it seems likely that any large adjustment of the complement of a species' acoustical neighbors would surely result in an adjustment of one sort or another in that species' calling sound.
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Several experiments have been done on interspecific song discrimination. Walker (154) showed that females of the two tree crickets cited above, *Oecanthus quadripunctatus* and *O. argentinus*, were able to discriminate their own species' song, and by juggling pulse rates and temperatures until the females responded to the wrong species' song, he further showed that the discrimination was based solely on rate of delivery of pulses in these simple trills. Perdeck (122) demonstrated that two grasshopper species (Acridinae) are able to discriminate one another's songs, and that this is a most important factor in preventing hybridization where the species overlap. Alexander & Moore (9) showed that two species of sympatric, synchronic cicadas are unable to respond to each other's songs because of their wide differences in both frequency and rate of delivery of temporal units. Roth (136) and Kahn & Offenhauser (89) demonstrated species differences in mosquito responses. An important study bearing on this question is the demonstration by Wever & Vernon (164) that an American *Gryllus* species (probably *pennsylvanicus*) has an abruptly lowered auditory threshold at just the frequency (pitch) of its song (ca. 4.5 kps.) This cannot be an accident, and one immediately speculates that other crickets must have their auditory organs similarly "tuned" to their frequencies. This means that the frequencies of rhythmically similar songs in different genera of crickets could be so different as to render the two kinds of songs almost inaudible between species belonging to the two different genera. In other words, although not selected in the context of reproductive isolation, frequency differences could be the effective distinction between songs; in such cases the rhythm patterns could evolve without reference to one another. For example: songs of Nemobiinae (ground crickets), which often live with field crickets, are usually pitched between 8 and 10 kilocycles per second.

I believe that all demonstrations of identity in acoustical behavior among allochronic and allopatric species of arthropods, and all demonstrations of interspecific acoustical incompatibility involving closely similar species, are cited above.

**PHONORESPONSES AND AGGREGATION**

Perhaps the most widely observed and easily demonstrated acoustical response in all arthropods is that which Busnel and his co-workers (31, 45) refer to as the "phonoresponse"—the production of sound upon hearing a sound. This behavior takes several forms, varying from a simple "reply" to the sound of a conspecific individual, or repeat of it (usually involving male calling sounds or aggressive sound only) to a consistent, rhythmic alternation or synchronization of calling phrases between males for indefinitely long periods of time. Specialized alternation and synchronization of calling phrases by Orthoptera and Cicadidae can be observed easily in many species in almost any part of the world, and in some cases have been analyzed in some detail (3, 9, 29, 31, 66, 68, 87, 88, 123, 130, 140, 159).

Curiously, no function has yet been demonstrated for phonoresponses
when they involve, as they do in most cases, two individuals of the same sex. Four possibilities can be suggested (3): (a) elaboration of the role of auditory feedback in rhythmical, long-continued calling of individual males may have incidentally rendered them "captive" phonoresponders to close neighbors in many species; (b) two or more males singing in alternation or synchrony may produce sound more regularly for longer periods of time (make up a more stable sound-producing unit) than lone-singing males because of stimulative and inhibitory effects upon one another [Barlow (16) has commented on a similar possibility for synchronous firefly flashing]; (c) phonoresponses may assist in the formation and maintenance of aggregations of males in situations in which individual males increase their chances of securing mates by joining such groups; and (d) rhythmic interaction (chorusing) by numerous males within a restricted area may prevent obscurement of the species-specific and female-attracting portions of the song or even enhance their distinctiveness. It can be seen that these four possibilities represent possible stages in the evolution of complex phonoresponses, and that the last three involve pair formation by way of specialized aggregations of calling males.

To demonstrate that any of the above functions has been elaborated as a result of selective action would be difficult. But the circumstantial evidence is often impressive, as can be illustrated with the 17-year and 13-year cicadas. Alexander & Moore (9, 10) demonstrated that individual males are stimulated into song by hearing tape recordings of calling males (and evidently would be similarly stimulated by hearing neighbors), and that in a synchronizing species with a song consisting of two parts alternated with one another, males hearing only part one of the song will respond by producing part two, and vice versa. They also found that most mating takes place within groups of chorusing males, and that males are attracted to the calls of other males. To the human ear, the rhythm of individual song phrases is more discernible when chorusing synchrony is achieved in those species showing it. The fact that one calling male stimulates another to call indicates that two males calling together make up a more stable sound-producing unit than one alone. In other words, every one of the above four functions is strongly suggested by these data on periodical cicadas, though none can be proved to have developed as a result of direct selective action.

Recently, Wynne-Edwards (169) has advanced another "explanation" for elaborated phonoresponses, namely that "mass-stridulation" as illustrated by choruses of crickets, cicadas, and katydids (as well as mass performances by male fireflies and males of many other species) ought to be viewed as "epidiectic" behavior, which he defines as concerned chiefly with dispersing the males and "regulating" the population density (or size, for he uses the terms more or less interchangeably), by which he evidently means specifically keeping it from going above a certain point. Wynne-Edwards uses as a principal argument the fact that other explanations have not been available for these phenomena, which is a doubtful justification even if it were not true that he cites only papers thirty or more years old on this subject. It is sur-
prising that the fallacies in his schemes of selection to account for this and other phenomena have not been more widely recognized [but see (166)]. In this case it will suffice to point out that the chorusing of periodical cicadas, which he specifically cites as a principal example: (a) renders the populations more dense, not less (for the effect is aggregation, not dispersal); and (b) presumably is chiefly responsible for increasing the size of the population, not decreasing or otherwise “regulating” it (since mating success is largely restricted to choruses in those species with the more elaborate chorusing behavior). Both of these facts are the reverse of what would be necessary to support Wynne-Edwards' hypotheses. It is perhaps appropriate to note here that he has made similar errors in dealing with the behavior of other insects. Thus, territorial and aggressive behavior in crickets is most pronounced during times of low population density rather than high (4); likewise, the apparent functions are increases in the reproductive potential of their possessors, not decreases. Among other things, Wynne-Edwards has erroneously lumped the territoriality of crickets, which seems to be functional solely in obtaining a mate, with that of birds and other parental animals which must obtain not only a mate but sufficient territory to provide for food and the other necessities involved in rearing offspring. When cricket populations are dense, aggressive behavior disappears, and is even replaced by a clustering—(4)—; no evidence yet exists to support the idea that adult behavior has been selected in connection with the dispersion of subsequent generations.

**Aggression**

Elaborate fighting behavior associated with special acoustical signals is known among arthropods only in crickets. Sounds evidently causing separation of individuals have been described in Crustacea (78, 126) Tettigoniidae (140, 143), Acrididae (51, 74, 85), and Passalidae (Coleoptera) (11). In Acrididae, such sounds have been termed the “rivals' duet” when a male intrudes during courtship of a female by another male, and “copulation song” when the intrusion occurs during copulation. The only detailed examination of the effect of aggressive acoustical signals in arthropods is that of Alexander (4), who summarized his findings as follows:

The aggressive stridulation of the males of Gryllinae is distinct from the sounds made in other situations. Stridulation by one male during combat usually causes the other male to stridulate, and in most species, both males stridulate during intense aggression. Dominant males stridulate during aggression more frequently than subordinate males, and the dominant male in an intensively aggressive encounter nearly always stridulates after antennal contact has been lost through the retreat of the subordinate. The subordinate male rarely chirps after an encounter, and if he does, it signals an impending change in his status.

A relatively specific set of artificial stimuli, such as simultaneous playback of aggressive sounds and simulated antennal lashing, is required to elicit the full display of aggressive behavior in a male unless he has just stopped behaving aggressively after winning a fight, is behaving territorially, or has just copulated. In such
cases, a male can be stimulated into aggressive activity with either tactile or auditory stimuli alone, indicating a temporary "conditioning" or "priming" effect. . .

Recent losses decrease a male's inclination to fight, and the dominance status of two males can be reversed over and over again by "defeating" the dominant repeatedly between encounters by means of artificial stimuli. Fighting or retreat is induced more quickly when aggressive sounds are played as the male is lashed with bristles simulating cricket antennae, and conditioning is stronger.

**Courtship**

Courtship signals can be defined as those occurring after pair formation and culminating in copulation or insemination when the courted individual is sexually responsive. This definition means that in some species courtship signals must be absent, and this is a reasonable prediction, based on the supposition that some courtship functions can be accomplished during pair formation and others may be absent in certain species. The independence of pair formation and courtship in some cases in which courtship is in evidence, has been noted by Haskell (75) as being demonstrated in Acridinae by the fact that if a pair is formed by chance meeting, calling or pair-forming signals are omitted, the sexual sequence beginning instead with the courtship signals. This seems to be true in all of the groups discussed below in which acoustical courtship signals are known.

According to the above definition, no acoustical courtship signals are known for any female arthropod. Acoustical courtship signals by males are known in Acridinae, Oedipodinae (Orthoptera: Acrididae), Gryllidae (Orthoptera), and Cicadidae (Homoptera), and are presumed on good evidence in crabs (137), and certain bugs (84, 99), and on rather scanty evidence in numerous other insects, including Drosophila (153).

Responses to courtship signals are difficult to demonstrate, partly because they seem often to be no more than "allowing" the male to copulate (for example, in both cicadas and grasshoppers). The presence or absence of such readiness to copulate, as a specific reaction to courtship sounds, must be tested, using normal and silenced males; such tests have not been performed. But Haskell (76) tested the responses of deafened and nondeafened grasshopper females (Acrididae) to male calling stridulations and attempts at copulation. Deafened females did not allow copulation, while nonoperated females did; there were no sham-operated controls.

The only other demonstration of response to courtship sounds is that of Alexander (3, 4) for field crickets (Gryllus), which indicated that females are caused to walk forward without directional orientation unless tactual stimuli are present. Ordinarily, this would cause the female to touch the rear end of the courting male and walk up on his back into the copulatory position. Artificial playbacks to a group of sexually responsive females caused them to locomote more or less without direction and to antennate one another when they came into contact, so that pairs of females often walked in circles around one another; presumably, if either of two such females stopped walking, as a male in that situation would, a copulatory position would be assumed be-
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between them. Coinciding with this evidence is my (unpublished) observation that when a male field cricket is placed with several females and begins to court, one can identify the sexually responsive females with a high degree of confidence as those which begin immediately to locomote.

Generally speaking, courtship signals have three possible contexts of significance: (a) they may be selected as reproductive isolating mechanisms in cases in which the chances of accidental pair formation are high; (b) they may be responsible for timing inseminations or insemination bouts by informing the individuals in a pair when both are sexually responsive; (c) they may facilitate insemination directly by moving the pair into the copulatory position. All other possible effects of courtship signals, as defined above, such as “bringing the female into a sexually responsive state,” or “causing the female to recognize males of her own species,” can be subsumed under these three headings.

The presence or absence of specific courtship signals in the sexual sequence of a species may be related to the above three effects. Thus, if several congeneric species live together so that the chances of interspecific pair formation are relatively high, we should expect to find courtship signals in at least all but one (probably all) of the involved species. Further, courtship signals selected in this context ought to be about as species-specific as the pair-forming signals. Species-specific courtship signals, however, do not necessarily denote a reproductive isolating function: the species-specificity may merely be a result of the derivation of the courtship signals from calling signals that are species-specific as a result of direct selective action (5). For example, if the pulse rate is about the same in all of a cricket’s signals and its calling song is caused to change under selective pressure associated with reproductive isolation, then the courtship song (as well as all the other signals in this case) will have to make the same change. It is also possible that a signal can be species-specific as a result of selective action that is no longer operating, for example, if a courtship signal once was the principal species-isolator, but the calling signals subsequently became species-specific and prevented all interspecific pair formations, or if a species no longer lives with another species which was potentially confusing to it and from which its courtship signals had diverged on this account. The significance of species-specificity must always be evaluated in terms of the particular species group involved. The same questions, incidentally, must be asked about all characteristics functioning late in the mating sequence and showing some species-specificity—for example, genitalic differences among species.

Courtship signals, then, may be expected to be vestigial, rudimentary, or absent when few congeneric or confusingly similar species live together, and when, in addition, accidental pair formation is minimal and pairs are formed only briefly in association with one or a few copulations. In the latter case, the pair-forming signal itself would accomplish the courtship function of timing inseminations. If pairs are maintained through successive inseminations or successive bouts of insemination, then courtship signals ought to be
expected as timing devices. If pair formation normally occurs through unori-
ented locomotion or without specific signals (in other words, accidentally),
then courtship signals should be expected in the timing function.

We can test the predictive value of these generalizations by applying
them to specific groups of arthropods in which courtship signals are known.
Thus, among arthropods with acoustical signals in their sexual behavior, an
extreme of long-term pair formation involves a social beetle in the family
Passalidae, Popišius disjunctus (Illiger), in which the pair isolates itself and
rears its offspring, with the adults living two or more years. Juveniles possess
stridulatory organs of independent origin from those of the adults, but prob-
ably their sounds are perceived by the adults' auditory organs, and vice
versa (11, 70). Unpublished observations on courtship behavior (Laura
Berkeley, personal communication) indicate that a special courtship signal
does occur, even though this species has lived for some time in North America
without relatives, even in the same family. The pair-forming mechanisms
are still unknown.

Various crickets maintain pairs through several copulations (4, 5). West
& Alexander (163) thought that in the subsocial species, Anurogryllus muticus
(De Geer), females copulate but once and then ensconce themselves in a
burrow from which they exclude all other crickets and lay their eggs and
bring in food which their newly hatched offspring consume. Subsequent
unpublished observations on this and a South African species indicate, in-
stead, that a female will copulate several times in one session, at intervals of
fifteen minutes or so, but will not copulate following some unknown period
after one or more copulations; in other words, after she has ensconced herself
in the brood chamber. A. muticus possesses a distinctive courtship signal
(163), even though no species in the same genus or otherwise potentially
confusing to it, occurs with it in North America, and evidently not in Central
or South America either.

Most of the crickets that are known to copulate several times in succes-
sion possess acoustical courtship signals. Alexander (5) lists eleven of fifteen
studied genera in this category; among the four remaining, courtship is not
clearly known in one case, and metanot al glands producing chemicals during
courtship occur in two cases, replacing acoustical signals (in one of these,
Hapithus, the female also eats the male's wings during copulation. Alexander
erred in omitting reference to metanotal glands possessed by this species). In
one genus, Cyrtoxipha, lacking both glands and a courtship song, the single
observed copulation took place extremely rapidly, without evidence of any
specific signals by the male.

Among Cicadidae, courtship signals have been sparsely known. One
would predict that Tibicen species in eastern North America, on the basis of
relatively low population densities and few species living together, should
provide a contrast with the Magicicada species which live together in great
abundance in groups of three species over most of their range. Present evi-
dence suggests that this is true. Alexander and Moore (unpublished data)
have discovered that all *Magicicada* species have two courtship signals which are always or nearly always produced in succession prior to copulation; no courtship song is yet known for any *Tibicen* species, although it must be admitted that the members of this genus have not been studied thoroughly, and Alexander & Moore (9, 10) did not discover the true nature of the acoustical courtship signals in *Magicicada* until the sixth year they studied periodical cicadas in the field.

**Post-Copulatory Behavior**

Three kinds of signals have been described which should be considered in this category. Among crickets and grasshoppers, sounds that closely resemble aggressive stridulations are produced whenever courtship is interrupted. No function has been actually demonstrated for these signals, but it is probable that they call back departing females if the interruption was accidental or have the usual aggressive effects upon other males if the interruption was caused by intrusion.

In many crickets, specific stridulations occur following each copulation, or perhaps more properly between copulations in a “bout” of copulations (3–5). Two functions are evident. First, females involved in the behavioral interaction including this kind of signal, are kept with the male until he has produced another spermatophore. Alexander (6) notes that the female among some crickets is ready to copulate again before the male. This function is very much like the timing function of courtship signals described above, but the two classes of signals are not necessarily alike: courtship and post-copulatory signals are similar in Oecanthinae; aggressive and post-copulatory signals in most Gryllinae; and calling and post-copulatory signals in *Miogryllus* (Gryllinae) and *Anurogryllus* (Brachytrupinae) (6).

The second function of post-copulatory signals in crickets is evidently preventing the female from removing the spermatophore before insemination is complete. Huber (82) found that females of *Gryllus campestris* did not remove the spermatophore until about 15 minutes had passed even when isolated from males, and that this was sufficient time for emptying of the spermatophore. However, there is no way to determine the delaying effect of the disturbance created by the separation, and it is significant that many orthopterans, in which the spermatophore ampulla remains outside the female, have a mucous mass or cap on the spermatophore. In the subfamily Gryllinae, this cap appears only in *Gryllodes sigillatus* Walker among crickets so far studied, and there are two noteworthy specializations associated with it: (a) the post-copulatory behavior of the male is weak, contact being lost between a pair in laboratory cages more frequently than in other Gryllinae; and (b) the female turns immediately following copulation and without interference from the male bites the cap off the spermatophore and chews it slowly and for several minutes. In other Gryllinae any movement by the female of the sort involving spermatophore removal causes a quick forward lurching and antennation by the male, this stopping further action by the female.
In certain Acrididae (51, 76), the male often stridulates during copulation, apparently when the female's movements or intrusion by another individual threaten disruption of copulation. This signal seems to be analogous to the post-copulatory signals of crickets, since its function is apparently maintenance of the pair until insemination is completed. The essential difference is that the genitalia are engaged while this is going on in Acrididae; in effect, the male holds the ampulla or bulb of the spermatophore while the female is being inseminated, while in most (but not all) crickets, the male inserts the spermatophore tube and immediately disconnects from the female's genitalia and the spermatophore. In most crickets with post-copulatory signals, insemination occurs after the genitalia have been disconnected, though in tree crickets the female remains on the male's back. The analogy between grasshoppers and crickets is furthered by the fact that in some grasshoppers the male rides on the back of the female without the genitalia engaged either before or between copulations.

**Food and Nest Site Directives**

As mentioned earlier in this review, one of the most prominent and stimulating series of investigations on animal behavior in this century has been that begun by von Frisch on the communication of honey bees more than forty years ago (60), and best known now from his 1950 and 1957 books (61, 62) and the subsequent book by Lindauer (102). Numerous papers have been published on this subject since von Frisch's books [for example, von Frisch & Lindauer (64); Lindauer (104)]; but only a few are pertinent here. The investigations of von Frisch, Lindauer, and others have shown that honey bee workers returning from distant sources of food vibrate their abdomens during the straight run portion of a "dance" during which a figure eight is roughly traced out by the bee. Direction of the food source (or potential hive site in swarming bees) is roughly indicated by the angle of the straight run relative to the perpendicular, which averages about the same as the angle of the food source relative to the direction of the sun from the hive. This relationship between angle with regard to a light source on a horizontal surface and angle with regard to the perpendicular on a vertical surface is a familiar component of the light-compass reaction known to exist in many arthropods (53). The additional speciality of the bee's dance is that the distance of the food source was found by von Frisch to be roughly proportional to the time taken by the bee to complete its figure-eight run. Subsequently, von Frisch & Jander (63) and Wenner (160) discovered that the length of the straight run itself is a more accurate reflection of distance. The angle of the dance remains accurate by virtue of continual shifting during the day as the sun moves, a shifting which continues even in bees that are not being exposed to the sun at short intervals. Bees in north temperate climates (with a southern sun) shift their dance angles counterclockwise and bees in south temperate climates shift their dance angles clockwise. Some intriguing results have been obtained by investigators interested in the problems of the
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sun passing through the zenith in a few days' time, and in what happens to northern bees transported to southern climates and vice versa (90, 119, 120), but, unfortunately, the results do not all agree (91, 103, 104).

Some of these studies are peripheral to the subject of this review, but I present them because of their relationship to the following curious fact. Although several investigators have indicated that the particular bees receiving the message about food source or potential hive sites can be recognized because they run alongside or behind the dancer with their antennae either being struck by the vibrating abdomen or touching the thorax of the dancer (several commercially available movies can be used to illustrate this behavior), no investigator has yet discovered what classes of stimuli are actually received by these presumed "responder" bees and how each is used. Even more curious is the fact that no one has presented data based on marked bees proving that particular "responder" bees have indeed received specific information as to distance and direction of food sources.

Wenner (160) analyzed statistically the best data presented on this topic (63), and concluded that because bees visiting wrong locations were not destroyed, a clumping of visits at the right post based on multiple scent post visitations was not precluded. Furthermore, the training of bees to feeding sites involves two odors, one provided by the experimenter and one added by the bees (Starzelduft) (104); precisely how these variables enhance the information received during dances, and therefore the extent to which there is correspondence between what humans have been deriving from bees' dances and what another bee can derive, seems to have been measured less accurately than is generally supposed.

Dancing bees make a noise when they waggle the abdomen, which Esch (48) and Wenner (160) found to be pitched at 200 to 250 cycles per second and made up of pulses of sound delivered at 35 to 40 per second. Wenner found this rate to be from 2 to 6 times the rate at which the abdomen struck a tiny cellophane flap glued to the microphone and held to one side of the bee's abdomen during wagging, and could not account for this rate. The number of sound pulses per burst, however, correlated as closely with distance as any other feature of the dance. Lindauer (104) refers to sound as a characteristic of more "vivid" dances, resulting from food sources of a high quality, and he refers to the acoustical part of the waggle dance as "additional (secondary) vibrations of the abdomen." He does not cite Wenner's (160) paper.

Heran (170) found that honey bee antennae are most sensitive to vibrations at the frequencies of sounds produced during the dance (162). Lindauer & Kerr (105, 106) believed that tibial receptors (perhaps the subgenual organs) are receptors for such vibrations in stingless bees. Otherwise, the mechanics of any possible sound reception as well as that of sound production are still completely unknown. It may be significant that other work with the effects of acoustical stimuli on honey bees has indicated that substrate transmission is almost mandatory. Wenner (161) caused a virgin queen bee
to "pipe" in response to an artificially produced imitation through the substrate but was unable to secure a reaction to more intense air-transmitted vibrations.

Lindauer & Kerr (94, 105, 106) found that workers of the stingless bees in the genus Melipona can alert members of the hive and cause them to locate food sources in greater numbers as a result of a buzzing noise (varying between 326 and 588 cycles per second among several species) made in the hive, which must be transmitted through the substrate. Bees in one compartment of a hive were alerted by buzzing workers in another compartment, and bees on soft substrates could not alert other bees.

The only other work on the question of the effects of acoustical stimuli on Apidae has been that of Hansson (73), Jarvis (86), and Frings & Little (59), who were able to stop the activity of honey bees by subjecting them to extremely intense sounds between 300 and 1000 cycles per second.

CONCLUDING REMARKS

This review has been highly selective, as was hinted in the introductory remarks. I have concentrated strictly on communicative functions of acoustical signals. Recent studies on hereditary aspects, developmental influences, effects of environmental variables such as temperature, and sensory, muscle, and neurophysiology have been almost entirely ignored. For information on these subjects prior to 1961, the reader is referred to Busnel (24, 25), Frings & Frings (54), and Haskell (76), and the reviews by Alexander (7, 8) covering the years 1961 and 1962. Haskell (77), Dethier (38), Roeder (134), and Huber (83) furnish recent reviews on related topics.

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