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INVERTEBRATE BIO-ACOUSTICS

1962

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(Copied from Bio-Acoustics Bulletin 3(3 & 4)

General

Fifty titles were compiled for this review, including three missed from 1961, three published by title only and included for the reader's convenience (44, 45, 175), five published as abstracts, and one not seen by the reviewer (54). The results of two pertinent symposia appeared during the year, one on insect acoustics held at the 11th International Congress of Entomology at Vienna, August, 1960, and one on cricket biology held at the Purdue (Indiana) AIBS meetings in August, 1961, co-sponsored by the Society for the Study of Evolution and the Entomological Society of America. In his introduction to the Vienna symposium, Haskell (67) provides a review of progress and problems, emphasizing unanswered questions in four areas: defensive behavior, sexual behavior, communication among social insects, and the role of acoustical behavior in speciation. Haskell, as with Alexander (3), seems to be stressing the necessity of "getting on with the business of understanding how species live." This means extensive observational, descriptive, and comparative study of behavior, and, as much of the material in this review attests, it seems to be the only way that many of the critical gaps in this field are going to be filled and many of the nagging questions and controversies put to rest.

New Instances of Known or Suspected Sound Production

Adams (2) suspects that the lacewing, Meleoma schwarzi (Banks) stridulates during courtship abdomen-wagging by rubbing striae on the second abdominal sternite against inner femoral tubercles. The Neuroptera are one of the few insect orders for which stridulation had not been previously suspected. Schaefer (131) discussed development of the so-called axillary spur on the metathoracic wing of 71 bug species (Hemiptera) in four families: Coreidae, Cydnidae, Urostylidae, and Pentatomidae, and concluded, contrary to previous speculation, that it is not a stridulatory device. Nachtwey (119) elaborately described a dorsal thoracic structure of some ants which he firmly believes is an ultrasonic signalling device. Mason(97) discussed the presumed stridulatory mechanism in juvenile and adult stone crickets (Schizodactylidae: Schizodactylus), concluding that in juveniles and

brachypterous adults, it is femoro-abdominal, while in macropterous species it changes to femoro-tegminal in the adults. This family represents a part of the Tettigonioidea which lost both the tibial auditory organ and the tegminal stridulatory device associated with it (some lost only the latter), and one wonders what they are doing with another kind of stridulatory apparatus.

Up to this point, no author had reported actually hearing a sound, or, in fact, actually observing a living insect. Wilkinson (173), in contrast, described and illustrated a stridulatory device on the head and prothorax of the females of three bark beetles (Ipidae), which in held beetles results in a sound with a frequency spectrum between 2000 and 16000 cps. He noted that males lack the apparatus and make no noise in the same situation. McCambridge (98) noted that another bark beetle, the Black Hills Beetle, can be sexed by stridulatory differences too, but in a completely different way. Males stridulate rapidly when held between the thumb and forefinger and struck lightly on the abdomen with a dissecting needle. Females usually do not stridulate, or they stridulate very slowly. Of 565 individuals tested, only 14 males did not stridulate and only nine females stridulated rapidly, for an overall four per cent error in sexing by stridulation.

DuMortier (36) added a new touch to an old kind of entomological paper by describing the stridulation as well as the anatomy of a gynandromorph shield-backed grasshopper which caught his attention in a group of caged females because of its acoustical behavior.

Signal Analysis and Physiology of Sound Production

Forrest (52) reported recording sounds of 25 species and varieties of ants, and indicated that sounds are different in different genera and may be species-specific. Although ants produce sounds by joint-snapping, "foot-scraping," and mandible-rapping, the most complex sounds are produced by stridulation in Ponerinae and Myrmecinae.

Shorey (138) used an elaborately padded chamber and sensitive recording apparatus to pick up the wing vibration noises of Drosophila melanogaster Meigen, which consisted of pulses of sound at 150-300 cps., delivered at rates varying more or less linearly between 25 and 40 per second at 22-32° C., with a temperature rate change of 1/4 - 1/2° C. per minute. Although Shorey drew no conclusions, there seems to be little doubt that this sound is not an auditory stimulus to the female, but that visual perception of the wing movements instead is involved.

Salmon and Stout (130) described and analyzed by audiospectrograph, sounds produced during courtship by the crab, Uca pugilator Bosc., by striking its large cheliped against the substrate in bursts of five or six thumps, individual thumps delivered within groups at rates (extrapolated) of 15-20 per second, and groups of thumps separated by intervals of about 0.3 sec. (about two bursts per second). They believe this sound functions when the female can no longer see the male's display chelipeds as he backs into his burrow,

and are convinced that no stridulatory sounds are produced by this species during courtship. Salmon (129) found that males begin sound production at dusk and continue until dawn. Frequency and intensity are increased when a female is brought near, when sounds of another male are played back, or when the male's leg is touched gently. Playbacks during the day induced males to come out of their burrows and wave, and increased the frequency of waving in males already waving. Promasov and Romanenko (122) described feeding and threat sounds produced by Black Sea crabs, postulating that the former attract other crabs through substrate vibrations and the latter cause defensive reactions. Hazlett and Winn (68) discussed methods of sound production in four genera of Bermuda crustaceans and illustrated the rasps of the spiny lobsters, Panulirus guttatus (Latreille) and P. argus (Latreille), and the shrimp, Alpheus armillatus Edwards, using both audiospectrograms and oscillograms for the first two species. Unfortunately, they used the narrow band filter on the spectrograph and so did not present the more informative picture that is possible with the wide filter for sounds in which maximum temporal resolution is desirable. A great many investigators studying arthropod and amphibian sounds apparently have not yet made this discovery. Hazlett and Winn found that crustaceans sonify more during the night, and they describe detailed observations on sound production during aggressive and territorial behavior.

Moore (104) and Nakshbandi and Zahlan (111) analyzed songs of Fidicina pronoe Walker and Cicadrata sp., respectively, using audiospectrograms and oscillograms, respectively. Both analyses would have been greatly enhanced by diagrams giving the reader an idea as to the nature of a complete pattern of song, such as those included by Alexander and Moore (6) for the various species of Magicicada. Two goals must be served by any analyzing instrument: (1) precision in the quantitative description of significant portions of the signal, and (2) maximal communication to the reader in the translation of an acoustical signal into a visual one. There is no longer any question about the vast superiority of the audiospectrogram for the second purpose, regardless of the kind of animal sound involved. The oscillogram usually excels in the former regard; but neither instrument portrays some sounds adequately, and it is often desirable to employ pen-and-ink diagrams.

Loher (91) found that removal of the corpora allata in females of the slant-faced grasshopper, Gomphocerus rufus L. (Acrididae: Acridinae), either during the last nymphal instar or within 24 hours following the molt to adulthood, prevented the females from responding positively to males, copulating or laying eggs. Ovariectomized females, allatectomized males, control females, and allatectomized females implanted with corpora allata from normal females four weeks following the molt to adulthood, all carried out normal sexual activities, including normal egg-laying in the last two cased. Allatectomized females showed reduced ovaries at the end of the investigation.

Wakabayashi and Ikeda (165) made extra- and intra-cellular recordings of action potentials and miniature electrical oscillations (MEO) in the tymbal muscles and studied oscillographs of the sounds of the cicadas, Graptopsaltria nigrofuscata (Motschulsky), Oncotympana maculaticollis (Motschulsky), and Tanna japonensis (Distant). They concluded that the tymbal muscle of each species has a characteristic interval of response which is apparently responsible for repetitive action potentials following single shock, and which "is liable to" synchronize with repetitive stimuli delivered at similar intervals or multiples of that interval.

Huber (72) reviewed recent work on the physiology of the nervous system in invertebrates, including hearing and the control of stridulation and other kinds of sound production. Huber's other paper (73) will be a welcome treat for those who have been wishing to see a discussion in English of his remarkable work on the nervous system of crickets and how it operates in connection with stridulation. His experiments with brain stimulation and nervous system ablation have indicated routes for certain impulses and localization of functions in the cricket brain. It is interesting that only calling and fighting sounds can be elicited by brain stimulation; courtship sounds have not yet been elicited, and may require stimulation of the large cercal (posterior) ganglion. Huber's work also suggests that different rhythm elements in a cricket's chirp may depend upon the mode of function of different parts of the central nervous system, which correlates with an interesting finding by Bigelow and co-workers (see reference in Alexander, (4) that similar rhythm elements segregate during hybridization and backcrosses involving species with different kinds of songs.

Pringle (121), in classifying cicada songs, noted that differences between genera probably stem from qualitative differences in one or more of the three muscle systems involved in tymbal vibration and differences between congeneric species mainly from differences in the patterns of nervous excitation of the various muscles. The tymbal muscle may be asynchronous (fibrillar) (Platypleura), synchronous (non-fibrillar) (Graptopsaltria, Tanna, Magicicada, and other genera), or intermediate (Meimuna).

Effects of Temperature

Walker (167) published a beautifully documented paper settling many of the persistent questions concerning the effects of temperature, humidity, air currents, and other factors in the physical environment on cricket sounds. Briefly, he showed that humidity, air currents, ageing, and temperatures during development have little or no effect upon a cricket's stridulation; light intensity differences may turn the songs on or off, but do not change their structure; and environmental sounds within the narrow range in which similarity to the species' sounds occur may affect

the sound in certain predictable ways, depending upon the species (for example, some species synchronize, some alternate). Aside from the effects of changes in behavioral situation, individuals' songs vary extremely little. The strongly dominant frequency in cricket stridulations is, as many investigators have previously suspected or to one degree or another demonstrated, a result of the rate at which stridulatory teeth are struck. Rate of delivery of rhythm elements and cycles per second (frequency) both increase with temperature increases, and in general this is a straight line relationship as most authors have indicated. However, rate of teethstrike (frequency in cps for the sound) does not increase linearly. Apparently because of the drag caused by contact between file and scraper during the acoustical (closing) portion of the wingstroke, there is a deceleration of frequency increase with temperature rise, a maximal frequency eventually being reached (maximal rate of passage of the file across the scraper). This deceleration is compensated to one degree or another by an accelerating rise in speed during the non-acoustical portion of the wingstroke, with a more or less linear change in overall rate of wingstroke (opening and closing strokes combined) being the result. Strokes may also be shortened at higher temperatures. Walker's data were drawn from studies of 19 cricket species involving seven genera and five subfamilies, and this work has no counterpart for any other insect group.

Frings and Frings (53) studied the effects of temperature on the song of the common meadow grasshopper, Orchelimum vulgare Harris. Unfortunately, they chose to use for analysis the song characteristics (repetition times for complete units of alternating "chipping" and "buzzing" sounds) which the animal varies according to behavioral situation. Thus, visual stimulation affects the number of chips produced: night-singing individuals often emit chips entirely, closely confined or aggregated groups of individuals may chip indefinitely without buzzing, and slight movement near a singer almost invariably increases chipping time. Further, groups of singers synchronize buzzes and use chipping time as the buffer for maintenance of synchrony (all of these facts had been noted in previous publications dealing with this species). This does not invalidate the Frings' graphs, which show overall an essentially linear relationship with temperature change, but it does explain their frequent referral to large, puzzling, and unexpected variations. Even in isolated individuals, one expects the most variation to occur in those features of the sound which are varied according to different behavioral situations. The most appropriate plots, particularly for the detailed and critical attempts at comparison with other investigations, would have been of pulse (wingstroke) rate, which they note in the introduction is probably the significant item to the female. A quick plotting of data from their table on this parameter ("pulse and pulse-silent cycles") shows less variation than in any other characteristic they studied (S.D. = 4-11% of the means) and an almost linear, slightly accelerating rate of

change with temperature increase, of the same sort as is being recorded for other Tettigoniidae in more casual studies (cf. 153).

Studies on Hearing

Belton (14) published a brief review of mechanisms of hearing in insects, and Schwartzkopf (134, 135, 136) extensively discussed the physiology of hearing in both insects and vertebrates. Busnel and Burkhardt(24) studied the reactions of nerve preparations of Locusta migratoria migratorioides (L.) to high intensity sounds, and emphasized the initial amplification of response brought about when sounds with sudden onsets (transiency) are used. They concluded, in line with comments in this review last year, that a minimal transiency is essential to induce reaction, and that the effect of transiency is principally one of initial arousal and not in itself species-specific information in insect sounds. Howse (71) concluded that the subgenual organs of termites and cockroaches respond to deviations from steady state conditions rather than to constant pressures (with regard to substrate vibrations).

Belton (15) found that the pyralid moths, Anagasta kuehniella (Zell.) (a flour moth), Ostrina nubilalis (Hbn.) (European corn borer), and Galleria mellenella (L.)(wax moth) all respond to high audible or ultrasonic frequencies in several ways. Tethered moths may stop flying or start to fly; moths at rest move their antennae or wings; immobilized moths may contract abdominal musculature and protrude the tympanal organs located on the ventral surface of the first abdominal segment. These organs are anatomically distinct from those on other moths, and Belton found them to be insensitive between 2,000 and 18,000 cps, even at a sound level of 90 db. Believing that pyralid tympana may enable moths to escape bats, since their susceptibility to high audible or ultrasonic frequencies is about the same as that of the corresponding organs in the noctuids studied by Roeder and Treat, Belton broadcast a sound "resembling that produced by a single bat" over experimental plots of corn from mid-June until the corn was mature. He states that the number of larvae in the stems and ears of about 1000 plants was reduced "by about 50 and 60 per cent." No indication is given as to what size area was examined or with what the counts were compared.

Wishart, van Sickle, and Riordan (174), in an intensive, careful study of the reactions of male yellow fever mosquitoes to sounds resembling those of females, concluded that direction orientation by response to either intensity gradient or Doppler effect does not occur. Normal response involves use of both antennae, and they believe that "a mosquito 'homing' to a sound orients itself until the microphonics from complementary parts of the Johnston's organs are in phase or until all cancelling-out effect is eliminated and the strongest combined stimulus reaches the point of central interpretation."

Each antenna has a strikingly low sensitivity to sounds directly in front of it. The antennae are moved actively during repsonsive flight, with a minimal measured angle of divergence of 46^0, and the investigators do no believe the mosquito would be responding to the sound in the position where it is least stimulating.

Roeder (127), Treat (161), and Roeder and Treat (128) have added impressive data to the development of their ideas on acoustical detection and evasion of bats by moths through (1) detailed study of bat noises as heard through moth tympana, (2) careful observations on the behavior of moths flying near lights as bats approached, (3) studies of the behavior of free-flying moths in the presence of artificial ultrasonic pulses, and (4) comparisons of catches of moths at ultrasonic and silent light traps. The data are generally positive, but often not as clear-cut as the authors would like. For example, Treat (160) found that moth species without tympana also favored the silent trap, and Roeder (127) found that lacewings (Neuroptera) also responded to ultrasonics, although they are not known to have tympana or to sonify. Roeder's experiments were so complex and so carefully designed that one hesitates to criticize, nevertheless, attention is drawn to the following: (1) his failure to indicate how intense the sounds were (for instance, see Busnel and Burkhardt (24) for the nature of the so-called "phonokinetic" response "...a non-oriented motoric reaction, usually of great amplitude and provoked by sounds of high (90-95 db.) intensity...can be released in an animal, but also on isolated parts of such...(for locusts) the thorax alone, without head, legs, abdomen or wings will show a phonokinetic reaction even when the tympanum is destroyed..." (2) his failure to indicate the number of tests, the percentage giving positive results, and the exact nature and number of control experiments; (3) his failure to describe the locations of the various lights with regard to the sound source (in view of the diving flights one wonders but cannot interpret what is meant by the "floor-light"); and (4) his erroneous statement that Treat's results with "deaf" (atympanate) moth species were negative. Although Roeder notes that oriented as well as non-oriented responses seem to be given when sounds are generated -- the former at longer ranges and lower intensities -- he does not seem to consider the possiblity that responses to the various lights turned on during the experiments simultaneously with or immediately following the generation of sound (in addition to the original flood-lamp) might also be in the nature of a "bewildering array" both oriented and non-oriented as well as sometimes absent.

In connection with the selective advantage of the ability of moths to hear bat cries, Treat (162) discussed the reasons for moth ear mites invariably infesting (and thus destroying) only one of the two tympana of their host. He concluded that the first mite takes the path of least resistance to either the right or the left tympanum and sub-sequent mites follow a chemical trail and perhaps also a physical trail of short duration caused by the first mite's disturbance of the body pile of the moth.

Communicative Interactions

Strübing (145) published excellent oscillographic analyses of the sounds of male and female planthoppers (tiny auchenorrhynchous Homoptera in the Family Delphacidae), and described male and female interactions during sound production. The sounds are surprisingly complex, and in many cases males have two sounds, one of which induces an alternating of songs with responsive females and probably is solely responsible for pair formation. A second courtship sound is often produced intensively just before copulation. Some species also make noises when disturbed.

Wenner (170) found that honeybee workers produce a pulsed sound at about 200 cps during the straight run of the waggle dance, and showed that the number of sound pulses per burst and the straight run sound production time correlate quite closely with distance of the food source. Sound pulses seemed to be delivered at a rate about 2.6 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 waggling. This is 1.3 times the rate at which the waggling abdomen changed direction, or about 35 sound pulses per second. Wenner believes that "waggling and sound pulses are not produced by the same muscular activity." Readers will note that while Wenner and Esch (paper reviewed last year) obtained similar figures in sound analysis, Esch was unable to find a corrleation with distance or direction of food source. As Wenner notes, "If honey bees use sound in communication, the mechanics of production and reception have yet to be solved." Curiously, although it is clear that they use "dancing" in communication, the mechanics of production and reception of that have yet to be solved as well! In another paper (171), Wenner 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 imitations. Some indications of specificity in rhythm pattern were obtained. This is the first actual demonstration of acoustical communication in honey bees, although, as Wenner notes in discussion, Lindauer and Kerr had already demonstrated substrate-transmitted signals in stingless bees.

Alexander (4) attempted to reconstruct in some detail evolutionary changes in the structure and function of the acoustical communicative system of the cricket. This is probably the best-known acoustical system in any animal group, and 90 species were utilized in this comparative study. It is postulated that the system developed from an original, short-range courtship signal in the ancestor of crickets and katydids, that calling (coming-together) signals evolved as out-growths of courtship signals, aggressive signals as out-growths of calling signals, post-copulatory (staying-together) signals as out-growths of calling and courtship signals in different groups, and

presumed "recognition" signals possibly as an outgrowth of courtship signals. Pathways of structural change and changes in the nature of information-carrying units are also postulated. Alexander (5) briefly listed some of the special problems in unravelling the mode of operation of cicada songs, and Alexander and Moore (6) described in detail the similarities and differences among the songs of the six species of 17-year and 13-year cicadas and how they function. They noted that the male songs bring about aggregations of sexually repsonsive individuals, and that most copulations occur in so-called "chorus" trees, which in the case of the least abundant species may be only a few trees in the forest. They believe that 17-year and 13-year cicadas may largely have lost the ability, seen in other cicadas, to adjust their acoustical behavior in conjunction with gross shifts in population density. This may be an important element in restricting them to an evolutionary pathway of specialization in which the minimal number of adults for success in reproductive behavior is great compared to other species.

Acoustical Behavior and Systematics

Many of the papers in this review in one way or another utilized acoustical behavior in classification (3, 6, 7, 121, 145, 153, 166), and others involved the comparative approach that the systematic attitude is largely responsible for bringing to bear upon an increasingly wide variety of biological problems (4, 15, 52, 68, 71, 72, 131, 134, 167, 173). Alexander (3) described the potentialities and limitations of the use of behavioral study in the classification of crickets commenting in particular upon acoustical behavior. Walker (166) utilized acoustical behavior as well as all other aspects of biology and morphology available in a definitive study of the tree crickets of North America (of which the second and final part is now in press). Alexander and Walker (7) located by their songs, two crickets new to North America one from the West Indies (Gryllus assimilis (Fabricius)) and one apparently from Japan (Scapsipedus micado Saussure). Thomas and Alexander (153) utilized acoustical behavior in a clarification of the relationships of three meadow grasshoppers long confused by orthopteran taxonomists.

Economic Applications

This essentially new dimension was included not only by Belton's experiments on acoustical repellence of corn borers (15), but also by the widely publicized report by Swearingen and Mohler (147) to the effect that a sound resembling cricket chirps in the noise of taxiing Electra aircraft may be responsible for the obvious reactions of starlings to the planes, and thus for such major incidents as one crash taking 62 lives and one aborted take-off involving Electras during 1960. The postulation by Swearingen and Mohler that starlings

feed on crickets and are attracted to the Electras has caused a whole series of reactions, including a study reaching entirely different conclusions carried out by the makers of Electra engines and the eventual assignment of a U.S. fish and widlife research unit to study the problem. Many questions are involved, and it probably would be less than "cricket" to describe them or attempt to answer them here as the wildlife unit is preparing its report. But it is a curious fact that although these questions were first raised in 1961, there is no evidence in any of the various reports, including mimeographed progress reports, that any one of the several different laboratories and groups of people in this country who are expert in matters of insect acoustics, bird hearing, analysis and interpretation of animal sounds, and the like were (until very recently) ever consulted or asked to use their facilities to aid in this investigation. Not even the recent literature was consulted. One hour, and at the most one half day, of discussion and assistance with sound analysis would have solved practically all of the problems raised two years ago and at the least provided invaluable orientation for any investigation that might have been pursued. It makes one wonder if those blanks for the national register of scientific and professional personnel are really worth filling out after all.

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