A COMPARATIVE STUDY OF SOUND PRODUCTION IN INSECTS, WITH SPECIAL REFERENCE TO THE SINGING ORTHOPTERA AND CICADIDAE OF THE EASTERN UNITED STATES

VOLUME I

DISSERTATION

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By

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PREFACE AND ACKNOWLEDGMENTS

This study was suggested by Dr. Donald J. Borror of the Department of Zoology and Entomology of the Ohio State University. It was undertaken with no more specific purpose in mind than that of learning as much as possible about insect sounds, and allowing the work to expand in any direction that appeared interesting along the way. As it has turned out, the study has been largely a systematic comparison of the sounds, and an observational study of the behavior and ecology of the singing Tettigoniidae, Gryllidae, and Cicadidae of eastern United States.

It is not often that a study such as this one can be carried out by a graduate student, with the financial support and wide array of equipment that have been available to me during the past three years. For these, I am indebted to the Department of Zoology and Entomology, the Graduate School of the Ohio State University, and the Ohio State University Development Fund. Chiefly, however, I thank Dr. Donald J. Borror and Dr. Carl R. Reese who have been solely responsible for securing the funds and equipment I have used, and who have given of their time and attention far beyond what anyone could possibly have a right to expect. Throughout this study I have been constantly reminded of my good fortune in having an advisor as prompt, unselfish, and actively interested as Dr. Borror.

I am deeply indebted to Dr. Edward S. Thomas of the Ohio State

Museum who has, among other things, identified the Ohio Orthoptera and Cicadidae, described and identified songs, and told me when and where to go to find unusual or spottily distributed species. An unknown amount of material incorporated into this thesis had its beginnings in information picked up on two field trips with Dr. Thomas, to Carroll County, Ohio, and Neotoma in Hocking County, Ohio.

I also owe a great deal to Dr. B. B. Fulton of North Carolina State College, who has provided a tremendous amount of information, both through his prompt and excellent replies to my letters, and during the three days spent collecting with him and discussing insect sounds at Raleigh, North Carolina, in August, 1955.

I am grateful for the helpful and continuous interest expressed by such people as Dr. Dwight M. DeLong, Dr. Frank W. Fisk, Dr. Alvah Peterson, Dr. Wencel J. Kostir, Mr. Jeff Swinebroad, and many others. Special thanks are due to Thomas J. Walker, Jr., Elbert L. Sleeper, Robert E. Woodruff, and Jay A. Buxton, all fellow students with whom I have spent many hours both in the field collecting and recording, and in the laboratory discussing various problems that arose as the work progressed. Several of the photographs were taken by Walker, and some of the recordings utilized were made by him.

Finally, my wife, Lorraine, deserves a great deal of credit, among other things for her tolerance toward such occurrences as my spending most of the nights of July, August, and September in the field recording until one, two, or three o'clock in the morning.

I take this opportunity to thank all the people listed above, and the many others who have contributed toward the development of this study.

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INTRODUCTION

It is quite likely that insects were the first animals on earth to produce sounds with special organs. The earliest evidence of such ability is a fossilized orthopteroid forewing from Triassic strata at New South Wales, Australia, which bears a large, toothed vein similar to the stridulatory structures of some of the modern Orthoptera. This insect lived perhaps two hundred million years ago, over fifty million years before the appearance of modern birds and mammals.

Today the chorus of insect sounds goes relatively unnoticed in the midst of the intense and endless noises of civilization, but to primitive man it must have appeared as a terrific din. Some of our ancestors' first vocalized labels for specific objects may well have been for the most persistently audible and abundant objects around them, the singing insects. The injection of rhythm into man's music may have been influenced by insect sounds. According to Annandale (1900, 14)[1], the Malayan natives attract a cicada which they use for food by forming a circle in the evening and rhythmically clapping their hands together. The chant, often called the most ancient of human music, consists of similar or identical phrases repeated over and over again, with little or no change in pitch; the sounds of many of the singing insects are of exactly the same nature.

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1. The bibliography is divided into sections numbered 1-26. The arabic numerals after the dates in literature citations refer to the section in which the reference can be found.

The earliest art, mythology, and literature attest to man's early awareness of insect sounds. According to Myers (1928, 14), the early Chinese thought of the cicada as a symbol of music, while to the ancient Egyptians it was an object of religious significance.

Scientific interest in insect sounds dates at least to Aristotle (see Myers, 1928, 14) who over two thousand years ago separated two groups of Homoptera on the basis of whether or not they could sing. Today, a complete bibliography on sound production and perception in insects would contain several thousand references.

Until recently, studies of insect sounds had to be based on human auditory impressions. The human ear is a rather poor instrument for analyzing insect sounds, and many aspects of insect acoustics had reached somewhere near their limits without better methods of analysis, and objective means of comparison. Today, magnetic tape recording and electronic sound analysis have been developed to the point where they are quite useful to the insect acoustician. Unfortunately, man-made and man-appreciated sounds are quite different from those made and appreciated by insects, and modern recording and analyzing equipment has understandably been slanted toward man's side of the picture. Consequently there are as yet no instruments that could be considered ideal for dealing with insect sounds. Nevertheless, those that are available provide objective methods of comparing at least part of the characteristics of insect sounds, and allow communication between investigators studying different insects in different parts of the world. A recent surge of interest in insect sounds has occurred, both in Europe and in America, due to the development of such equipment.

The potential importance of studies on insect sounds is not likely to be over-emphasized. Applications are numerous, and exist in many phases of biology. Insect sounds have long been used in systematics, and in studies of ecological and geographical distribution; they show promise of being valuable in connection with control, and in fundamental studies of behavior and physiology. Insect acoustics is in the early stages of infancy and represents a relatively unexplored field for future research.

THE NATURE AND SIGNIFICANCE OF SOUND PRODUCTION IN INSECTS

What Insects Produce Sounds

Specialized sound production and perception are known or suspected in about 200 families of insects, representing 13 of the 26 orders. In many groups, such as certain families of Orthoptera, Homoptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera, both functions are known positively, and are practically universal; in others they are known or suspected in only a few or a single species. For example, Weber (1929, 11) found structures he suspected to be stridulatory organs in the hog louse, *Haematopinus suis* L., though this insect has never been heard to make a sound. Our knowledge seems far from complete, and it is entirely likely that we may eventually find that a majority of the insect species possess one or both of these abilities. The recent work of Ossiannilsson on Swedish Homoptera has clearly demonstrated that there may be thousands or tens of thousands of species whose sounds are so soft that they can be heard only if the insect is held practically inside one's ear, or if some sort of amplifying device is employed. I have acquired the habit of holding up to my ear almost every small insect that I collect. A surprisingly large number and variety of species produce some sort of "chatter" when held in this manner.

The following list of orders, families, and subfamilies has been compiled from the references in the bibliography at the end of this paper. Each group listed has been mentioned as containing one or more species either known to produce or perceive sounds, or possessing structures or behavior probably associated with these phenomena. The list is not complete, and the individual reports were not screened as to their probable accuracy. Except for some of the older references, the classification is essentially that of the individual authors. The starred groups are those which contain one or more species whose sounds have been recorded or heard in the course of this study.

A List of Insect Families Containing One or More Species Known or Suspected to Produce or Perceive Sounds

- Odonata
- *Orthoptera
  - *Acrididae
    - *Acridinae
    - *Oedopodinae
    - Pamphaginae
  - Blattidae
  - *Gryllidae
    - *Eneopterinae
    - *Gryllinae
    - *Mogoplistinae
    - *Nemobiinae
    - *Oecanthinae
    - *Trigonidiinae
    - *Gryllotalpinae
  - Mantidae
  - Phasmidae
  - Stenopelmatidae
    - Anostostomatinae
    - Lezininae
    - Prophalangopsinae
  - *Tettigoniidae
    - Agroeciinae
    - Bradyporinae

*Tettigoniidae, cont.
    - *Conocephalinae
    - *Copiphorinae
    - Ephippigerinae
    - Hetrodinae
    - Litroscelinae
    - Meconeminae
    - *Phaneropterinae
    - Phasgonurinae
    - Phyllophorinae
    - *Pseudophyllinae
    - Saginae
    - *Tettigoniinae
    - Tympanophorinae
    - Zaprochilinae
- Isoptera
- Plecoptera
  - Perlidae
- Psocoptera
- Anoplura
  - Haematopinidae
- Thysanoptera
- *Hemiptera
  - Corixidae
  - Gerridae
  - Naucoridae
  - Nepidae
  - Notonectidae
  - Piesmidae
  - Podopidae
  - *Reduviidae
  - Scutelleridae
  - Veliidae
  - *Corimelaenidae
- *Homoptera
  - Agaliidae
  - Aphididae
  - Areopidae
  - *Cercopidae
  - Chermidae
  - *Cicadellidae
  - *Cicadidae
  - Cixiidae
  - Coccidae

*Homoptera, cont.
- Eucanthidae
- Eupelicidae
- Euscelidae
- Idioceridae
- Issidae
- Jassidae
- Lednidae
- Macropsidae
- Megophthalmidae
- *Membracidae
- Ortheziidae
- Psyllidae
- Typhlocybidae
- Ulopidae

*Coleoptera
- Anobiidae
- *Anthribidae
- Bostrichidae
- Brenthidae
- *Carabidae
- *Cerambycidae
- *Chrysomelidae
  - Hispinae
  - *Criocerinae
- Cicindelidae
- Cistelidae
- Clytridae
- *Curculionidae
  - Barinae
  - *Calandrinae
  - Cossoninae
  - *Ceutorhynchinae
  - Cryptorhynchinae
  - *Hylobinae
- Dytiscidae
- Endomychidae
- Erotylidae
- *Elateridae
- Gyrinidae
- Haliplidae
- Heteroceridae
- Hydrophilidae

*Coleoptera, cont.
- Hygrobiidae
- Ipidae
- Languriidae
- *Lucanidae
- Megalopidae
- Nemonychidae
- Nitidulidae
- *Passalidae
- Pelobiidae
- Ptinidae
- *Scarabeidae
  - *Acanthocerinae
  - *Aphodiinae
  - Cetoniinae
  - Dynastinae
  - *Geotrupinae
  - Melolonthinae
  - Rutelinae
  - *Coprinae
- Scolytidae
- *Tenebrionidae
- *Trogidae

Lepidoptera
- Agaristidae
- Arctiidae
- Callidulidae
- Ctenuchidae
- Drepanidae
- Epiplemidae
- Eupterotidae
- Geometridae
- Hesperiidae
- Lithosiidae
- Lycaenidae
  - Lycaeninae
  - Nulitinae
  - Theclinae
- Lymantriidae
  - Acronyctinae
  - Coctiinae
  - Plusiinae
  - Sarrothripinae
  - Careinae

Lepidoptera, cont.
- Nolidae
- Notodontidae
- Nyctomeridae
- Nymphalidae
- Papilionidae
- Parnassidae
- Pieridae
- Pyralididae
- Saturniidae
- Sphingidae
- Sterrhidae
- Thyatiridae
- Thyrididae
- Uraniidae
- Zygaenidae

*Diptera
- Calliphoridae
- Chironomidae
- Conopidae
- Culicidae
  - Chaoborinae
  - *Culicinae
- Gastrophilidae
- Glossinidae
  - Drosophilidae
  - Limoniidae
  - Muscidae
  - Sepsidae
  - Syrphidae
  - Tabanidae
  - Bibionidae

*Hymenoptera
- *Apidae
- *Bombidae
  - Formicidae
  - Halictidae
  - Ichneumonidae
- *Mutillidae
  - Vespidae

How Insects Produce Sounds

Sound production and perception have arisen independently in the insects a large number of times, and consequently a wide variety of structures is involved. In general, "special" sounds are produced by insects in one or more of five different ways: (1) by rubbing one body part against another, or stridulation (Coleoptera, Lepidoptera, Hymenoptera, Orthoptera, and many others), (2) by vibrating some body part such as the wings in air (Diptera: Culicidae), (3) by striking some body part such as the feet (Orthoptera: Acrididae, Oedopodinae), the tip of the abdomen (Orthoptera: Blattidae), or the head (Coleoptera: Anobiidae), against the substrate, (4) by vibrating drum-like structures called tympana (Homoptera: Auchennorhyncha), and (5) by forcibly ejecting air or fluid (Orthoptera: Acrididae). The vast majority of insect sounds are produced with stridulatory mechanisms.

Pumphrey (1940, 26) discusses three types of auditory structures occurring in insects: (1) chordotonal sensilla associated with tympana (Orthoptera, Homoptera, Lepidoptera), (2) chordotonal sensilla associated with Johnston's Organ (Diptera), and (3) hair sensilla (Orthoptera, Lepidoptera).

Sound-producing and auditory structures may involve almost any part of the insect's exoskeleton. In different groups such organs have been found on the mandibles (Orthoptera: Acrididae), palpi (Orthoptera: Phasmidae), head capsule (Coleoptera: Anobiidae), pronotum (Coleoptera: Cerambycidae), mesonotum (Coleoptera:

Elateridae), metanotum (Orthoptera: Prophalangopsidae), forelegs (Orthoptera: Tettigonioidea), middle legs (Coleoptera: Lucanidae), hind legs (Coleoptera: Passalidae), forewings (Orthoptera: Tettigonioidea, Acridoidea), hind wings (Orthoptera, Coleoptera), several of the abdominal segments (Coleoptera, Hymenoptera, Orthoptera, Homoptera), and the cerci (Orthoptera). Many species possess two sets of sound-producing organs (Hemiptera: Corixidae), or auditory organs (Orthoptera: Gryllidae).

The males of Tettigoniidae and Gryllidae, the chief subjects of the present study, produce their sounds by rubbing together specialized structures on the forewings or tegmina (Plate I). A sharp-edged "scraper" projects upward from the inner edge of the lower tegmen and contacts a transverse row of tiny teeth called the "file," located on a heavy vein on the lower surface of the upper tegmen. Plates II and III show photographs of the tegmina of several species of Gryllidae and Tettigoniidae. The files can be seen as dark transverse lines near the base of the tegmina. The scraper is located on the median edge of the other tegmen, almost opposite the inner end of the file. The venation of both tegmina is usually greatly modified in the males as compared with the females which in these species do not possess tegminal sound-producing organs (Figures 11, 13).

Plates IV and V show drawings of the file and scraper in a cricket (Acheta domesticus L.) and a katydid (Amblycorypha oblongifolia (DeGeer)).

PLATE I. TEGMINAL POSITIONS DURING SONG IN TETTIGONIIDAE AND GRYLLIDAE

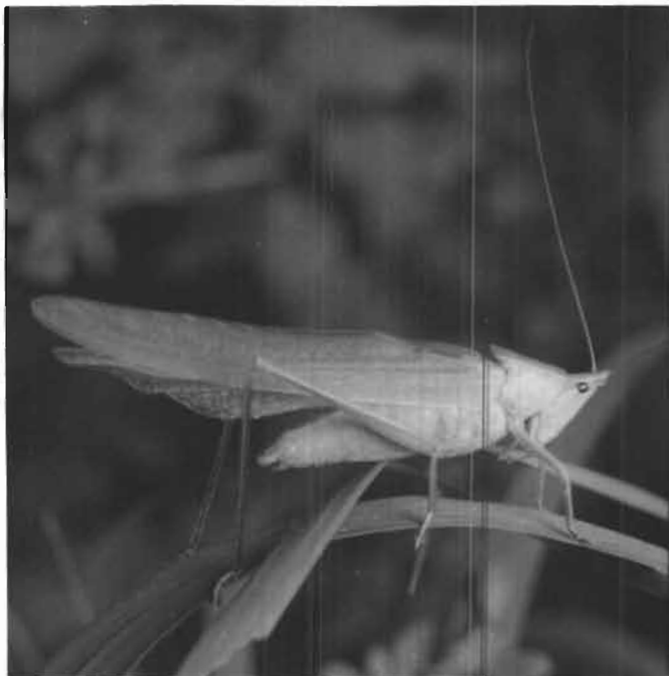


Fig. 1. Neoconocephalus at rest (tegmina in nearly this same position during song)

Fig. 2. Oecanthus producing calling song

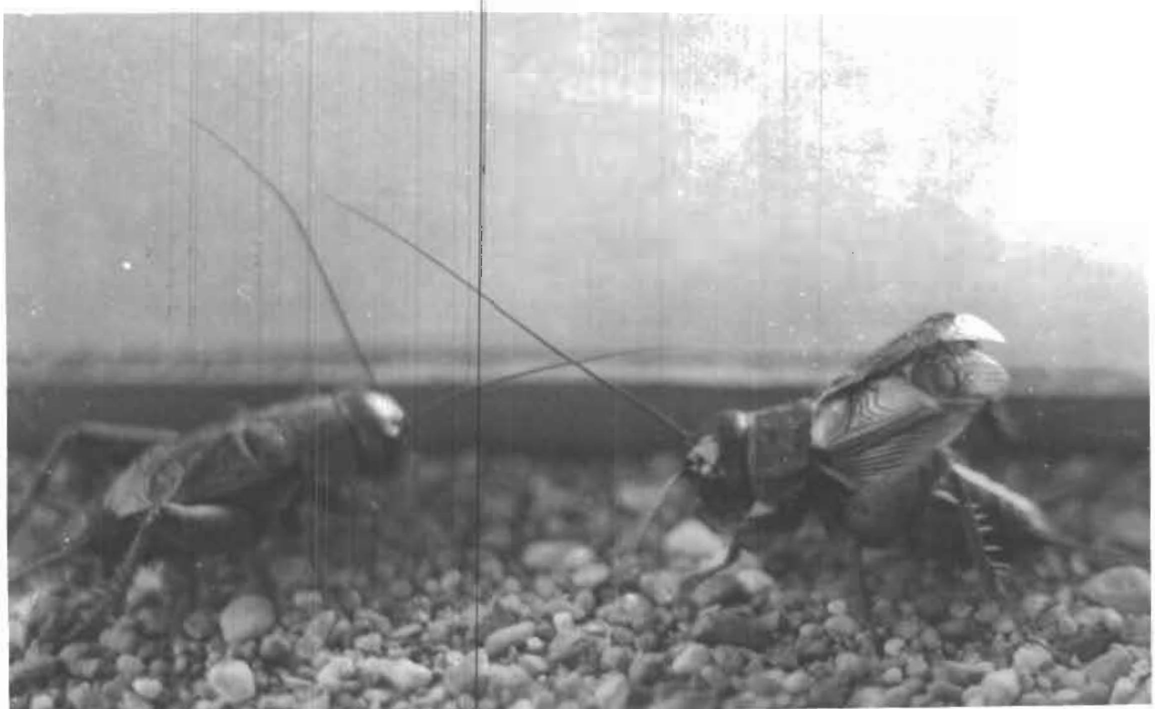


Fig. 3. Mountain Acheta at rest (left) and producing fight song (right).

PLATE II. TEGMINA OF MALE TETTIGONIIDAE (APPROX. $1\frac{1}{2}$ X NORMAL)

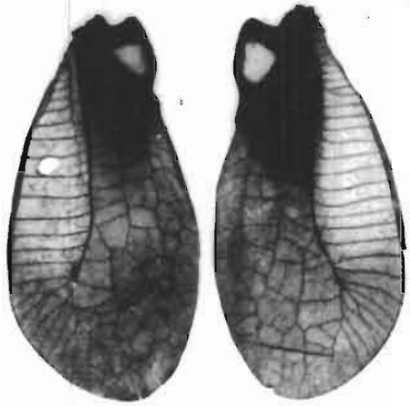


Fig. 4. Pterophylla camellifolia

Fig. 5. Atlanticus testaceous

Fig. 6. Amblycorypha oblongifolia

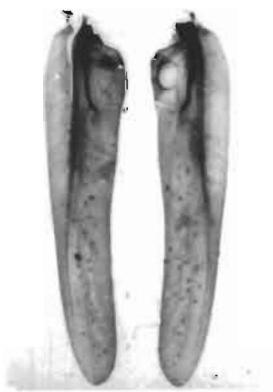


Fig. 7. Neoconocephalus retusus

Fig. 8. Scudderia texensis

Fig. 9. Scudderia furcata

PLATE III. TEGMINA OF TETTIGONIIDAE (MALE) AND GRYLLIDAE (MALE AND FEMALE)(APPROX. 2 X NORMAL)

Fig. 10. *Miogryllus verticalis*

Fig. 11. Northern wood *Acheta* (female below)

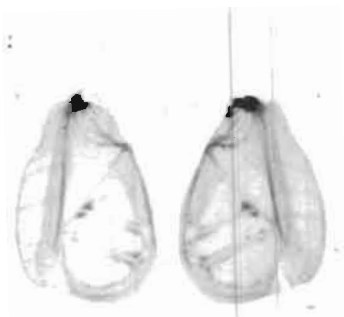


Fig. 12. *Oecanthus latipennis*

Fig. 13. Mountain *Acheta* (female below)

Fig. 14. *Conocephalus nemoralis*

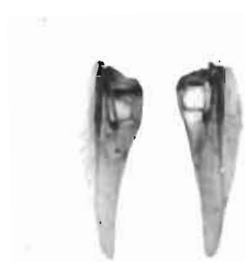


Fig. 15. *Orchelimum nigripes*

PLATE IV. TEGMINAL SOUND-PRODUCING STRUCTURES OF ACHETA DOMESTICUS L.

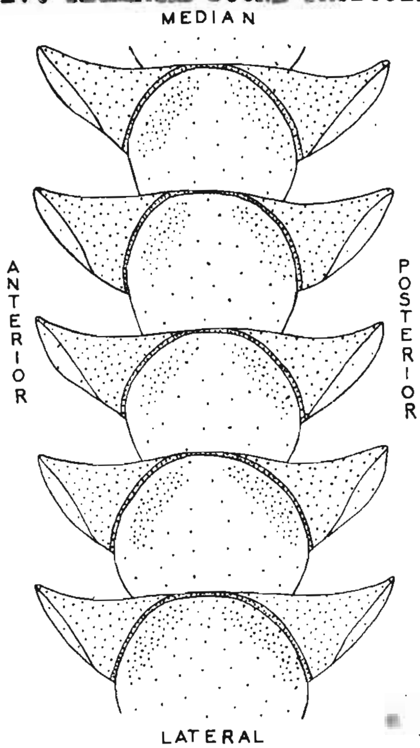


Fig. 16. Ventral view of file (40 teeth per mm.)

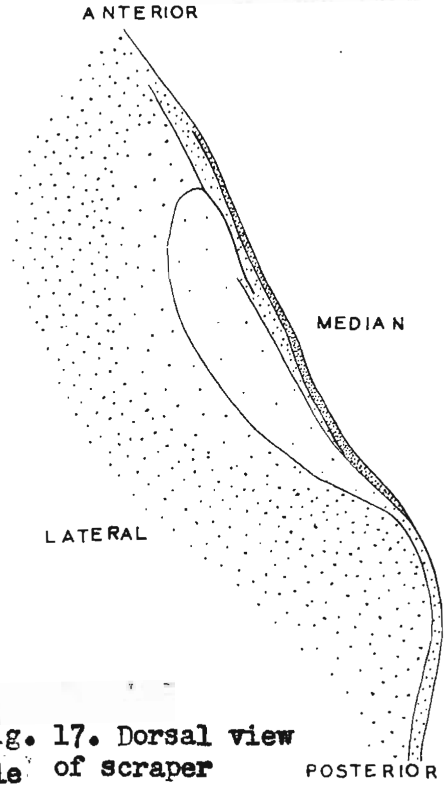


Fig. 17. Dorsal view of scraper

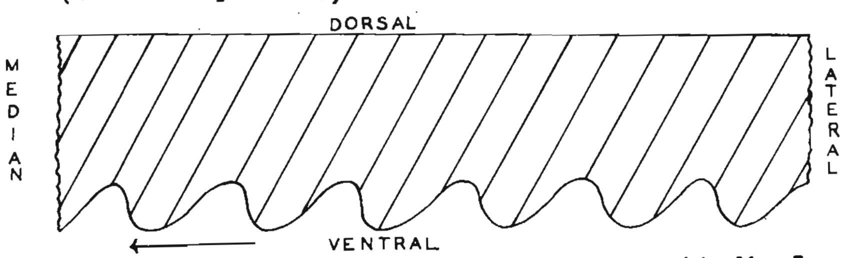


Fig. 18. Diagrammatic longitudinal-section through file

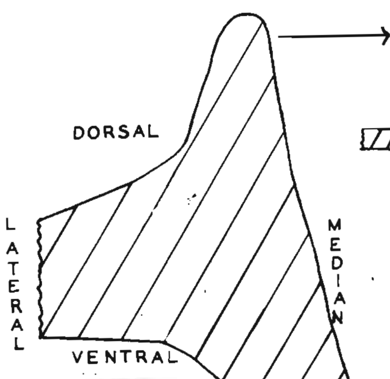


Fig. 19. Diagrammatic cross-section through scraper

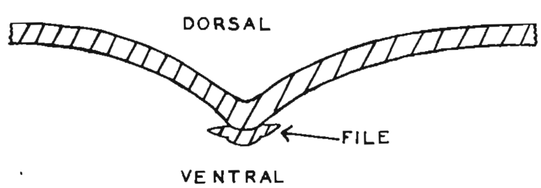


Fig. 20. Diagrammatic longitudinal-section through tegmen showing location of file

PLATE V.

TEGMINAL SOUND-PRODUCING STRUCTURES

<u>AMBLYCORYPHA</u> <u>OBLONGIFOLIA</u>

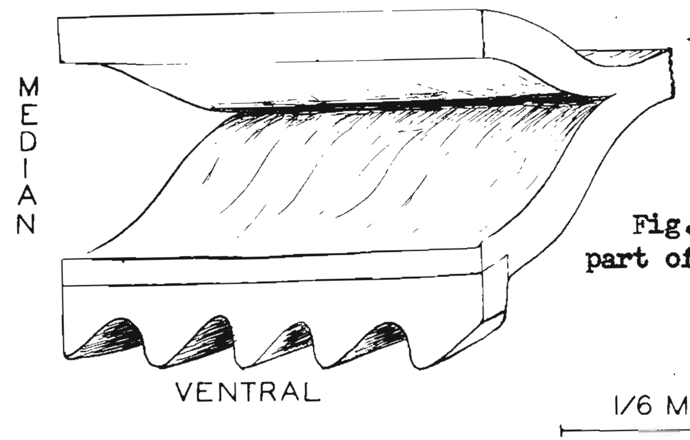


Fig. 21. Section through part of file

1/6 MM.

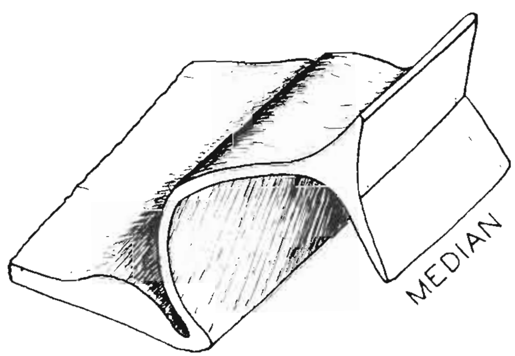


Fig. 22. PORTION OF SCRAPER

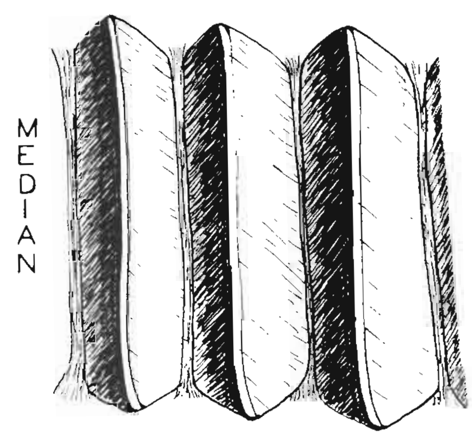


Fig. 23. FILE TEETH

When Insects Produce Sounds

Insects produce sounds in two general types of situations. First, there is a group of insects which includes the katydids, long-horned grasshoppers, crickets, some of the short-horned grasshoppers, cicadas, and leafhoppers, the adult males of which produce sounds more or less continuously throughout daily periods which are apparently determined by daily fluctuations in light intensity and/or temperature and humidity. The sounds produced by some of the insects in this group are the loudest and best-known of insect sounds, and because they usually consist of rhythmical repetitions of the same phrases over and over again, we have come to call them "songs." Since these "songs" are the sounds of these species which are most often heard, and they are usually produced by individuals which are alone, they have received such labels as "common" songs, "ordinary" songs, "solitary" songs, or "calling" songs.

The second general group of situations consists of those in which the sound is elicited directly by the presence or activities of other organisms. The sounds produced in such situations may be further divided into three categories: (1) those produced by males, females, or immatures as a result of the presence or activities of animals of some other species, usually disturbing, capturing, or holding them, generally called "protest" sounds, (2) those produced by a male in the presence of a female of the same species, generally called "courtship" or "mating" sounds, or songs, (3) those produced by a male in the presence of another male of the same species, generally called "warning," "intimidation," or "fight" sounds, and (4) those produced by a female in the presence of a male of the same species.

The Functions of Insect Sounds

The descriptive terms used above to label the various insect sounds are connected either with the situation in which we observe the sound produced ("solitary" song, "protest" sound), or with what we suspect to be its function ("warning" sound, "courtship" sound). Some sort of labels are necessary for purposes of discussion, and it is more meaningful to develop them in this manner than in any other. Less suggestive terms would probably not substantially reduce anthropomorphic interpretation or bias, and they would certainly be less communicative.

Nevertheless, it should not be forgotten that we have only guessed, and in most cases the actual behavioral significance of insect sounds remains to be demonstrated. In spite of detailed analysis of the sounds themselves, we are still largely ignorant as to which of their structural characteristics are significant, and what responses are elicited as a result of them. This statement is almost as true for birds, amphibians, and non-human mammals, as it is for insects.

In considering the question of the possible functions or behavioral significance of insect sounds, two questions arise: (1) can insects recognize their own sounds from those of other species they might hear, or in other words, can songs act as behavioral isolating mechanisms between species, and (2) can insects recognize, or do they respond differently to, the different sounds produced by members of their own species in different situations?

Many investigators have reported response by singing insects to crude imitations of their songs. Scudder (1868a, 6) claims to have been able to locate and capture singing Orthoptera by getting them to "answer" an imitation of their song. Allard (1911e, 6) says that he got an immediate response to an imitation of <u>Atlanticus</u> <u>testaceous</u> (Scudder). Beamer (1928, 14) reported that females of <u>Tibicen</u> <u>dorsata</u> (Say) alighted in great numbers on a Ford tractor driven through weedy fields in Kansas. According to him the engine noise of the tractor resembled the song of the male. Annandale (1900, 14) says that the natives of Malaya attract the cicada, <u>Dundubia</u> <u>intenerata</u> (<u>Pomponia</u> <u>intemerata</u> (Walker), according to Myers (1928, 14), by forming a circle around a fire in the evening and clapping rhythmically. Significantly, no response could be obtained later in the evening after the males had begun their singing. Myers (1928, 14) cites a large number of instances in which cicadas are apparently attracted or affected by clapping, singing, and other loud noises. Regen (1914, 6) found that females of <u>Gryllus</u> <u>campestris</u> L. moved toward a telephone receiver from which the song of the male was emanating. In 1926, Regen (6) reported that a Galton whistle, a bell, and the songs of other species interfered with the alternation song in <u>Thamnotrizon</u> <u>apterus</u> Fab., and that the "s" sounds of the human voice caused them to "answer." He was able to get males of this species to continuously alternate songs with an artificial partner. Pierce (1948, 26) found that a male of the northern true katydid, Pterophylla camellifolia (Fab.), would "answer" almost any sudden sound after he had first been stimulated by a played-back recording of his own song, and then subjected to more and more crude imitations. But Pierce noticed that this male always answered with the same number of pulses as occurred in the imitation, up to five, beyond which he apparently "lost count."

Dr. A. C. Perdeck of the University of Leiden, Netherlands, has found rather refined discriminatory capacities in two closely related species of slant-faced grasshoppers, Chorthippus biguttulus L. and C. brunneus Thumb. (unpublished data obtained through personal communication). The males of these two species "differ strinkingly in their song patterns," and according to Dr. Perdeck, the females of each respond with a high degree of selectivity to the song of their own species. Hybrid females are less choosy. This is apparently the only case in which a female insect has been demonstrated to "selectively" respond to the sound of the male of her own species while being simultaneously subjected to that of another. The work of Frank Blair (1955, 26) and A. P. Blair (1942, 26) on amphibians is of interest in this connection. Frank Blair found that in two closely related species of Microhyla which hybridize in a narrow zone of overlap and have distinct songs, the songs of the two species are more distinct in the area of overlap than outside it. He states that song is an important isolating mechanism in these species, and that in the zone of overlap there is selection against hybridisation and thus selection against those females which are less discriminative with respect to the songs of the two kinds of males, and for those males of both species which have songs most distinct from each other. A. P. Blair, on the other hand, concluded that song is an imperfect, if at all effective isolating mechanism in several closely related species of Bufo.

The results of work done by Busnel and his associates in France are in apparent disagreement with those obtained by Pardeck. These investigators used as one of their test species, Chorthippus bigut-tulus Thunb., one of the two species studied by Perdeck. They were able to get males of this species to respond to crude, mouthed imitations of their song to the extent of walking up the imitator's arm and even to his mouth as long as he continued to make the sound. Dr. Busnel has also found that in two species of Ephippigera which do not live together in nature, the females apparently respond as often to the sounds of males of the other species as to their own, and that a female will respond to an artificial sound rather than that of a male of her own species, if the artificial sound has about 10 db. more intensity. As a result of his investigations, Dr. Busnel has remarked in conversation that it may be possible that most or all of the females of singing insects respond equally or nearly so to all the insect sounds around them, losing interest in males of other species only upon coming within range of other senses, such as sight, smell, or touch.

The answer to the question of discrimination or lack of discrimination with respect to interspecific song differences may be reversed from one situation to the next. In localities where only one or a very few insects are active in song at a given time of day or year, it seems likely that little selective value would be attached to a high degree of specificity of response to the particular details of structure in the sounds. A possible explanation for the apparent disagreement in the results listed above is that a female in a sexually responsive state might respond to almost any sound characterized by sudden and great changes in intensity. But if two such sounds are produced at equal intensities she might respond only or most often to that one which contains the characteristics of the song of her own species. This would explain the apparent change in the response of females of *Pomponia intemerata* (Walker) to artificial sounds produced before and after the males had begun singing in the evening, as well as the apparent discrepency between the results of Perdeck and Busnel. However, nothing has been done to test this hypothesis with two species that occur together in nature.

In eastern United States, where hundreds of individuals in dozens of species may be singing simultaneously in a small woodlot or marsh, inability of females to recognize the song of males of their own species would result in "utter confusion," and this would perhaps be the most inefficient communicatory system in insects. There are definite indications that this is not the case, and that actually a high degree of selectivity occurs, with many or most species in this area recognizing their own sounds from all others they might hear.

The first indication that differences between the sounds of different species of insects may often act as behavioral isolating mechanisms lies in the fact that it is practically impossible to find two different species whose sounds cannot be separated. Many species are known, such as in the American Acheta, Anaxipha, Amblycorypha, Pterophylla, and the Oecanthus nigricornis group, which are distinguishable only by their songs, or by ecological, seasonal, or geographical distribution. More often than not, such closely related species have songs as distinct or even more distinct than those of morphologically well-defined species. This is purely circumstantial evidence, but it seems unlikely that song differences, if neutral with respect to selective value, would develop any more quickly than morphological differences.

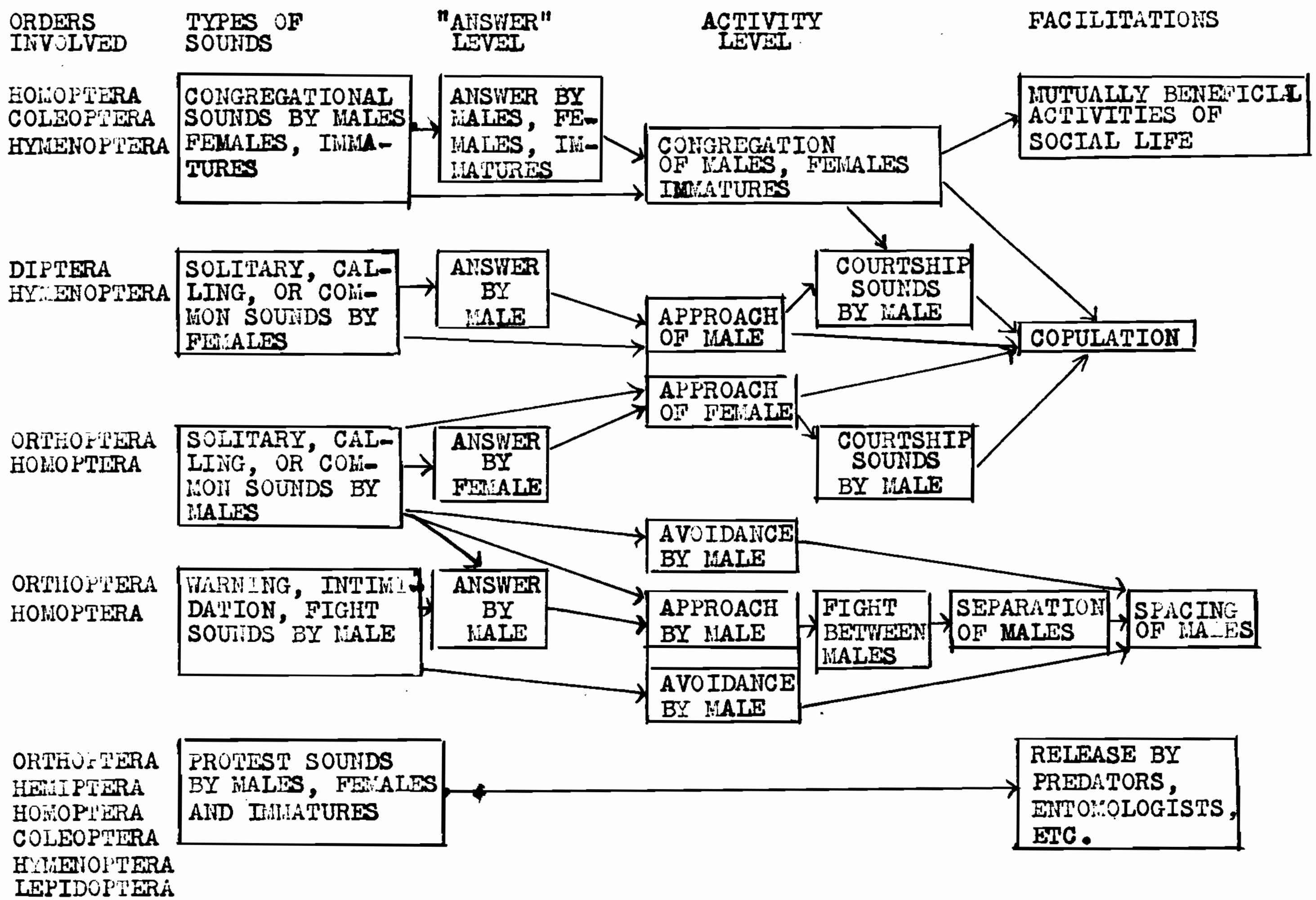
The second indication that insects recognize their own sounds from those of other species is in the alternation and synchronization of song between individuals of the same species, even when individuals of other species are singing nearby. This occurs in many Orthoptera (Fulton, 1934, 6) and indicates that these males distinguish the song of their own species from all others in the area. Some of the night-singing insects begin singing in the evening when many other species are already singing. Yet when the first individual begins to sing, the others in a colony chime in so quickly that as many as forty or fifty individuals may be singing only a few seconds later. In some of the night-singers which synchronize their songs, such as *Neoconocephalus nebrascensis* (Bruner), synchronization has been repeatedly observed to be present from the first chirp of the second individual to start singing, indicating that the near-simultaneous starting of song is not due to a high and uniform degree of sensitivity to climatic conditions. On the other hand, a rather dense and isolated colony of *Oecanthus niveus* (DeGeer) observed on several different occasions required several minutes after the first continuous singing in the evening to develop synchronization.

Even non-synchronizing species exhibit behavior that can only be explained by an ability to recognize their own song. In species such as *Atlanticus testaceous* (Scudder), *Amblycorypha oblongifolia* (DeGeer), *A. rotundifolia* (Scudder), and *A. uhleri* Stal, the individuals do not sing continuously or for long periods of time without pausing, but instead they repeat their phrases only a few times, then are silent for a few minutes before singing again. In the field, different individuals in these species do not sing independently of each other, but rather a colony sings in bursts which are separated by silent intervals in which none of the individuals in the colony are singing. This means that these insects must be stimulated by their own sounds rather than by the hundreds of other, and often seemingly more intense insect sounds around them. Hopkins (1898, 14) reported hearing a colony of the seventeen-year cicada burst into full song at midnight after one individual had given a loud "squawk." This species normally sings by day. Apparently the acoustic stimulus here was sufficient to completely overcome any inhibition caused by climatic conditions.

The third indication that relatively slight variations in insect sounds are behaviorally significant is connected with the variations that appear in the sounds of a single species or a single insect, and the question of whether or not such infraspecific variations have any significance for the individuals of that species. As illustrated in the part of this paper concerned with describing the songs and behavior of individual species, many insects, especially the crickets, produce a number of different sounds in different situations. Although these sounds sometimes grade imperceptibly from one to another, and are often very brief in situations that are of short duration, nevertheless a single individual, and all the individuals of a species, consistently produce the same sounds in the same situations. Often, the differences between the sounds of one species in several situations are very much like the differences between the sounds of another species in the same situations. After observing a culture of crickets for some time, one can tell by listening, and without looking, exactly what is going on in the culture, by the kinds of sounds being produced.

Plate VI shows the behavioral sequences that have been repeatedly observed in connection with the sounds produced by different groups of insects. Concrete evidence for cause and effect relationships in these sequences is generally lacking, but these are definitely implied, and the diagram is justified on that basis.

PLATE VI. BEHAVIORAL SEQUENCES ASSOCIATED WITH INSECT SOUNDS (Fig. 24)



Only five "kinds" of sounds are distinguished in Plate VI, and it will be noted that sounds suspected of having the same or similar functions sometimes occur in different orders. These are not homologous, and in many cases sounds with similar functions or occurring in similar situations have arisen independently a large number of times within a single order. In the Coleoptera, for example, "protest" sounds are produced by species in a large number of families by a variety of structures occurring on many different parts of the body, and certainly of different origin. In only two orders, the Orthoptera and the Homoptera, does sound production of common origin occur in two or more different families.

In some cases, sounds with similar functions have developed in different groups as offshoots of sounds having completely different functions. For example, it seems likely that the "protest" sound was the first to develop in the Cicadidae, and that any congregational or courtship sounds developed later. As will be shown later, the reverse is true in the Tettigoniidae and Gryllidae, with the original sound probably involved in a courtship sequence, and the protest note, in the two species in which it is known, having apparently developed later as an extension of the stimulus situation evoking the "fight" or "warning" sound.

Orthoptera: Gryllidae and Tettigoniidae

Solitary songs, as defined by the diagram (Plate VI), are well-known in the males of the Gryllidae and Tettigoniidae. Here these songs are apparently analogous to the so-called "territorial" songs of birds, the "advertisement" of the presence of a male in a particular locality, with significance to both the females and the other males of his species.

The males in the Tettigoniidae and Gryllidae tend to remain in the same spot, that is, on the same plant, in the same part of the same tree, or by a rock, fencepost, or burrow, all their adult lives. Male mountain crickets (Acheta assimilis Fab.) have been heard in the same spot for over thirty days. This sedentariness has also been noted in Pterophylla camellifolia (Fabricius), Neoconocephalus ensiger (Harris), N. nebrascensis (Bruner), Microcentrum retinerve (Burmeister), Orchelimum nigripes Scudder, O. silvaticum McNeill, Amblycorypha rotundifolia (Scudder), Conocephalus nemoralis (Scudder), and Oecanthus niveus (DeGeer). Specimens have not been marked and checked nightly, but in many cases this is not necessary. In several instances only a single individual of a species was ever heard in locations passed as often as four times daily for several weeks, and the song was always heard from the same spot. On visits extending over a period of several weeks to the Ohio State University woodlot and other areas in Franklin County, Ohio, given songs were repeatedly heard from the same spots. In a colony of a dozen singing males of Amblycorypha rotundifolia (Scudder), observed continuously for two hours, there were no changes in perches, the same songs continuing to come from the same spots. In many cases the songs of individual insects are recognizable because of unique characteristics.

M. Busnel (in Busnel, R. G., 1954, 6, p. 176) has marked males of Oecanthus pellucens Scop. and observed them for fifteen consecutive nights. She found that individual males have territories within which they remain, and which they "tour" at intervals and "defend" against intruding males of the same species.

The formation of colonies of singing males in the field, often apparently "within" habitats, and the spacing of singing males, indicates that the calling song also may attract another male that is some distance away, and repel those that are close by. Only on rare occasions have two singing males of the same species of Tettigoniidae or Gryllidae been found close together in the field, with the exception of such species as Nemobius fasciatus (DeGeer), N. socius Scudder, or Anaxipha exigua (Say). These are small species, and if they have territories, these would be so small that spacing would be difficult to observe. In large insects, such as species of Scudderia, Pterophylla, and Microcentrum, singing males are always several feet apart. Busnel says that the territories of individual males of Oecanthus pellucens cover around 30-50 square centimeters. In the most dense colonies of Atlanticus testaceous (Scudder) and Amblycorypha oblongifolia (DeGeer) singing males were from two to three feet apart.

When two males are found close together in the field, they are usually producing sounds which vary somewhat from their usual song. In Bath County, Virginia, two males of Pterophylla camellifolia (Fabricius) were heard only a few feet apart in a small tree, and they were alternating songs in quick succession. Each song contained

15-30 pulses or wingstrokes, as compared to the usual 2-6 pulses for other specimens in that area. In another case, while collecting specimens of Neoconocephalus robustus crepitans (Scudder) in an alfalfa field, a peculiar sound was heard. Upon approaching and turning a flashlight on the scene, two males of this species were seen on plants about six inches apart, facing directly away from each other, and singing "furiously." In the laboratory when one male field cricket or house cricket approaches another, especially if one of the two is singing the "calling" song, the sound produced is quite distinctive. Males of Orchelimum vulgare, O. nigripes, and O. concinnum caged together in the laboratory usually produce only the ticking part of their alternately ticking, alternately buzzing song. This may be an indication of the significance of this two-part song; one portion may attract the females, and the other repel nearby males.

The females of the singing Tettigoniidae and Gryllidae are "rovers," so to speak, and are much more often seen in the field than are the sedentary males. Many collections are composed almost entirely of females for this reason. The females are apparently attracted by the songs of the males and move toward, find, and eventually copulate with them on this account. While attempting to locate a singing male of Atlanticus testaceous (Scudder), I collected two females which were walking rapidly and steadily toward him from different directions. I have noticed a definite increase in the activity of a female of Oecanthus argentinus Saussure each time a male on the same plant produced the calling song. Regen (1914, 6) demonstrated that females of Gryllus campestris L. are directionally attracted by the song of the male, and Busnel and his associates in France have absolutely demonstrated this function in Ephippiger bitterensis. Sexually responsive females released in the vicinity of a cage of singing males made a "beeline" directly to the cage.

Fulton (1933, 6) observed a variation in the usual pattern of the males of Tettigoniidae being sedentary and attracting the females by their songs. He heard a soft noise in the vicinity of singing males of Microcentrum rhombifolium (Saussure), and discovered that it was being produced by a female of the same species. By listening and watching for some time he was able to determine that the male actually moved to this female who stayed on her perch and continued to make the soft noise he had heard. There may be some significance in the fact that the male of this species has two distinct songs, (Plate XLVI) for which the difference in stimulus situation has not yet been discovered. It is possible that a male changes from one song to the other upon hearing the sound of a female in the vicinity, and continues to make this second type of song while locating and approaching the female. In the field, the individuals in a given area seem always to be singing the same song. A male singing the "ticking" song in the field was captured and caged alone in the laboratory. Later he was heard producing the "lisping" song.

Protest sounds have apparently only been observed in a few species of Orthoptera. Males of the northern true katydid, Pterophylla camellifolia, stridulate continuously when held, and

Blatchley (1920, 6) reported that a male of Amblycorypha oblongifolia stridulated in his hand. A similar response has been reported for European Ephippigeridae.

Orthoptera: Acrididae

Very few original observations have been carried out on the Acrididae in the present study. Faber (1929, 1932, 1936, and 1953, 6) has studied both the Acridinae and Oedopodinae in Europe. His original classification of the sounds produced by Acridinae was as follows:

1. Gewohnliche Gesang (Common Song), produced by males and not dependent on the presence of individuals of either sex.

2. Rivalenlaute (Song of Rivals), produced by two males in close proximity.

3. Werbegesang (Courtship Song), produced by a male near a female of his own species and usually preceding copulation.

4. Paarungslaute (Pairing Song), produced by a male just before he leaps upon the female and attempts copulation.

5. Das Ubergehen von einer Gesangart zur anderen (Transition from one kind of song to another).

In 1953 Faber states that it is possible to distinguish among the Acrididae 19 different expressions, 14 of which are especially important. His enlargement over the previous classification involves chiefly the division of rivality and courtship into various phases which generally occur in sequence in these situations.

Faber, and Busnel and Loher (1953, 1954, 6) indicate that in the Acridinae sounds are produced by individuals of both sexes, and the male changes his song somewhat after hearing a response from the female, then moves toward her, stopping at intervals and emitting his sound, then proceeding again upon hearing the response of the female.

The sound communication system of the Acrididae is apparently quite similar to that of the Tettigoniidae and Gryllidae, in spite of the fact that these two systems apparently arose completely independently, as will be shown later, and the method of copulation is quite different in the two groups.

Many of the Oedopodinae stridulate in flight. This flight stridulation is associated with the exposure of brightly colored underwings which are completely hidden in resting specimens. As suggested by Blatchley (1920, 6), Morse (1907, 6), Isely (1936,6), and many others, this combination of sound production and bright colors seems associated with the congregation of individuals of both sexes, or with the attraction of one individual to another. Isely (1936, 6) in discussing several species of Oedopodinae which stridulate in flight, says "... resting out-of-sight individuals of the same species take spontaneously to the air in response to the flight song or rattle of another individual of the same species."

<u>Homoptera:</u> <u>Cicadidae</u>

Little is known of the exact function or functions of the sounds produced by "lone" male cicadas. The references by Annandale (1900, 14), Myers (1928, 14), and Beamer (1928, 14) to the attraction of females of various species by hand-clapping, tractor engine noise, and other sounds supposedly resembling the songs of the males, were mentioned earlier. Myers also cites a number of examples from the literature and from personal communication with others which indicate that the songs of male cicadas attract the females. Many of these are but casual observations, and there certainly has been no work on the function of cicada song anywhere near as convincing as that conducted with the songs of Orthoptera. Pringle (1954, 14) says, "The function of the song is to assemble the local population of a cicada species (males and females) into a small group. It remains to be determined whether it is the main intersexual stimulus in mating behavior."

Without doubt there is some deviation from the patterns which exist in the Orthoptera. Contrary to the sedentariness of male Tettigoniidae and Gryllidae, I have frequently seen males of _Tibicen chloromera_ (Walker) alight, sing once, fly, alight, sing once, fly, alight, sing once, etc., several times in succession. On the other hand, males of _T. linnei_ (S. & G.), _T. lyricen_ (DeGeer), _T. canicularis_ (Harris), _T. pruinosa_ (Say), and _T. marginalis_ (Walker) have been heard to sing for hours from the same tree without flying. In _T. auletes_ (Germar) and _T. resonans_ (Walker), both of which sing for only a short period of perhaps a half hour to three-quarters of an hour at dusk, the individuals of both sexes become very active at this time, the males singing in great numbers, and both sexes doing a great deal of flying about. While there may be sedentariness on the part of the male in some species, the idea suggested by Pringle and others, that of congregation of both males and females into close proximity, seems to fit most observations better than any other.

Sounds of a courtship nature, performed by the male in close proximity to the female and also by the female when near the male, have been reported in a number of species of Cicadidae. Swynnerton and Loveridge (1922, 14) describe a sound produced by the male of *Monomatapa insignis* prior to attempted copulation, and Pead (1910, 14) describes a similar situation for *Taipinga consobrina*. Myers (1928, 14) quotes correspondence with a Miss Marion Shaw who noticed a wing-clicking sound made by a female of *Melampsalta cingulata* near the male. Myers observed similar behavior in *M. muta*, *M. cingulata*, and *M. strepitans*. Pringle (1954, 14) recorded a "distinct courtship song" from a male of *Platypleura octoguttata* in close proximity to a female, and states that it ended with attempted copulation.

There is little evidence of a male "fight" sound in the cicadas analogous to that occurring in the Orthoptera. Perhaps the nearest to this is a statement by Beamer (1928, 14) concerning caged individuals of *Tibicen dorsata* (Say). He states that when a pair was copulating in the cage, other males could almost invariably be found crawling over the copulating pair and singing continuously.

Cicadas are well-known for their "protest" sounds. In all of the four species which I have been able to collect during this study the males produced loud "squawks" when captured and held. These sounds are often heard in the field, and if one's glance is quick enough the cicada will usually be seen flying, closely pursued by a bird or by the cicada-killing wasp, Sphecius speciosus (Drury). In Kentucky and southern Illinois I have watched this wasp capture cicadas, sting them, and fly off carrying them. Every time this was observed, the captured cicada, presumably males in each case, was heard to emit this loud, harsh sound.

Homoptera other than Cicadidae

Ossiannilsson (1949, 15) classified the sounds he heard produced by various species of Auchennorhyncha (excluding the Cicadidae) according to the system used by Faber (1929, 1932, 1936, 6) for the Orthoptera. In this classification he distinguishes a "common song" produced by the male "independent of the presence of other individuals of either sex," which seems to fall into the general category of calling song as defined here. He noticed both synchronisation and alternation between singing males. He believes the primitive condition with respect to this sound may be that in which the female also has a sound-producing organ and she "answers" the call of the male and he then moves to her. He further states (p. 134), "In most other species, however, the female has lost the capacity of answering by a call. Perhaps the male has now other means of finding her, or the female has taken over the searching role. Nevertheless the call of the male may have kept its original purpose as an enticing call in general."

Ossiannilsson describes the sound emitted by the female, observed in only one species, Doratura stylata, as a "call of invitation."

Ossiannilsson describes a sound he calls the "call of courtship," which he heard in three species, Paropia scanica (Fall.) (Megophthalmidae), Eupelix depressa (F.) (Eupelicidae), and Doratura stylata (Boh.) (Euscelidae). It was either emitted in conjunction with copulation, or just prior to copulation. In two species, Philaenus spumarius (L.) and Neophilaenus lineatus (L.) (Cercopidae) he observed sounds produced during the act of copulation. He called this sound the "call of pairing" and did not know whether it was produced by the male or the female.

With respect to male "warning" or "fight" sounds, Ossiannilsson states that he heard a "call of rivalry" from Achorotile albosignata (Dahlb.) (Areopidae).

Ossiannilsson heard sounds that he referred to as "calls of distress" in fourteen species of Auchennorhyncha, included in the families Cercopidae, Eupelicidae, Idioceridae, Macropsidae, Jassidae, Megophthalmidae, Ulopidae, Euscelidae. In some cases this sound was heard in both sexes; in other cases only the male was heard to produce it. He says that these sounds "are apparently emitted when the animals feel themselves in trouble of some kind, for example when they try to escape from their confinement. Not all of the above species, however, will emit this call if they are held fast.... I refrain from theorising about the significance of these calls. As they are so weak (in our species), they will hardly scare any enemy."

Ossiannilsson's work is probably the only work published on the biological significance of the sounds produced by Homoptera other than Cicadidae. In the course of this study I have picked up many species of Membracidae, Cicadellidae, and Cercopidae which produced soft "chattering" noises that could be heard if the insect was held close to my ear.

Hemiptera

Hungerford (1934, 13) describes a sort of courtship sound produced by males of the backswimmer, Buenoa limnocastris, prior to copulation. He says, "The male singles out a female, maneuvers for a position some distance beneath and behind her, and begins a ticking noise as he slowly cruises nearer....when within a half-inch or so of the female, the ticking changes to a hum, and is followed by a sudden dash to embrace her."

Protest sounds have been observed in two species of Reduviidae in this study, one of them an immature.

Coleoptera

Practically the only sounds known for Coleoptera are those that are produced by males, females, and often larvae as well, when they are captured, held, squeezed, poked, shaken, or otherwise disturbed, and which therefore fall into the category of "protest" sounds.

Ohaus (1900, 17) reports evidence of a congregational function in the stridulation of Brazilian Passalidae. He says that the scattered individuals of a colony disturbed by tearing its log apart stridulated almost constantly, and that a short time later he noticed four adults and two larvae under a small chunk of the log, stridulating, and two other larvae moving rapidly toward the chunk. I have noted a similar reaction in Cloeotas aphodioides, a small scarab beetle. Robert E. Woodruff collected several of these beetles from under bark where they were clustered in great numbers. They were placed in a petri dish and a ball of wet cotton was dropped in to supply moisture. Shortly after it was noted that a few individuals had burrowed into the ball of cotton and were stridulating loudly. Within a few minutes all the individuals in the dish were inside the ball of cotton, and when it was picked up they stridulated loudly. This observation may have little significance since many other things may have been involved, but it indicates the type of thing that might occur, and the ease with which it could be tested.

Lubbock (1888, 17) says that if a male death watch beetle ticks and there is a female within a few yards, she returns the tap and they approach each other slowly, tapping at intervals until they meet. Will (1885, 17) claimed that a male of Cerambyx scopuli grew restless and moved toward a box six inches away which contained a female being irritated with a pin to make her stridulate.

One of the beetles recorded in this study, the cerambycid, Tetraopes femoratus LeConte, produced two sounds when held. One of these was a loud squeak, produced when the beetle was being held between two fingers; the other was a low rumble produced when the beetle was crawling around inside my closed fist. A number of these beetles were collected and placed in a jar with a part of the milkweed plant from which they were taken, and this rumbling sound was later heard from the jar, although it had not been disturbed for some time.

Pferrer (1955, 17, unpublished M. S. Thesis) has reported hearing a sound made by the fungus-inhabiting tenebrionid beetle, Bolitotherus cornutus (Panzer), which apparently has a relationship to copulation. Her description is as follows:

> Prior to mating, the male beetle clasps the female in such a manner that the ventral surface of his abdomen rests on the dorsal surface of her thorax, and that the ventral surface of his thorax rests on the dorsal surface of her abdomen. When in this position, the male rubs the ventral surface of his abdomen across the two prominent tubercles which project from the female's thorax. This produces a characteristic rasping sound audible at a distance of six to eight feet from the fungus. This noise-making is carried on for one or two minute periods interspersed by one or two minutes of quiet. At the end of one of these periods of rasping, the male reverses his position and copulates with the female. This noise-making may be carried on at different periods for several days before and after copulation and during the egg-laying period. The noise is usually produced at night, but may be produced on cloudy days.

It seems unlikely that the soft sounds produced by beetles could function in bringing the male and female together from very great distances, but they could cause congregation of individuals within an area to which they had already been attracted by some other sense, such as smell. It is noteworthy that a great many of the beetles found to have stridulatory structures congregate in great numbers in small ecological niches, such as Closotus aphodioides, mentioned above, and many of the dung, carrion, and fungus-inhabiting beetles. The Passalidae are semi-social insects, and according to Miller (1931, 17), "The adults chew up the wood for food, both for themselves and for the larvae. The larvae can live without adult care, but become dwarfed, and the period of development is lengthened....Pupal case building is a cooperative affair between larvae and adults. The adults assist in the formation of the cases, especially the outside, and keep them in repair during the entire pupal period." It is not difficult to hypothesize a congregational function related to the sound production which occurs in larvae and adults both.

It seems surprising that no more work has been done on the behavioral significance of beetle sounds in view of the fact that probably more species in this order produce stridulatory noises than in any other group of insects.

Diptera

Certain of the wing-beat frequencies produced by female mosquitoes in flight, according to Roth (1948, 22), and Kahn and Offenhauser (1949, 22) are effective in attracting the male from great distances, and thus fall into the class of "calling" songs. Kahn and Offenhauser were able to attract more male mosquitoes in ten minutes to an "electrocution" screen set up in front of an amplifier reproducing the call of a female of Anopheles albimans than they could get in a cattle trap in a week. This work was done in a swamp near Havana, Cuba. Similar experiments performed in the laboratory with *Aedes aegypti* were also successful.

Ninety per cent of the mosquitoes attracted to the trap Kahn and Offenhauser set up in Cuba were males of *Anopheles albimans*, and the investigators state later in their summary that in general, the calls are specific, "*Aedes* will not respond to *Anopheles*, etc."

Interestingly enough, Kahn and Offenhauser believed that the sound also attracted frogs, chameleons, bats, dragonflies, and other predators of mosquitoes. Although there has been much speculation as to the possibility of the "mating calls" of insects also attracting their predators and parasites, this seems to be the only evidence for this phenomenon.

A number of investigators have made observations which indicate that in other families of Diptera the females may attract the males by vibrating their wings at certain frequencies, and vice versa. These are largely summarized by Rau (1940, 26).

Hymenoptera

Practically the only kinds of sounds observed in the Hymenoptera are those produced by disturbed, captured, or confined specimens, or "protest" sounds, some of which, in the ants and mutillids, have been suspected of having a congregational function. Peringuey (1899, see Mickel, 1928, 24) reports that McNeill was able to collect males of *Mutilla cleantha* and *M. hecuba* by holding the females in such a way that they stridulated. He claimed that the males would "...immediately appear and swarm around, and even settle on the hand of the captor..." Wheeler (1903, 24) thought that one of the reasons he could collect so many ants by burying a wide-mouthed jar up to its neck in the mound of the nest was because the stridulation of the first ants to fall in attracted other individuals. Later (1910, 24) he suggests that the vibrations which excited the ants may have passed through the substrate and not through the air.

One of the most discussed sounds of Hymenoptera is the "piping" of the queen honeybee. Comstock (1905, 24) says this noise is produced by a queen when she discovers another queen cell, and if the queen inside the cell is fully developed, she "answers" with a similar response. She also says this piping of the queen is evident before an after-swarm is about to issue, and when a queen is being "balled" by the workers. According to Ribbands (1953, 24), Landois (1867) was able to get queens to pipe by placing them in cages in close proximity to one another.

Pumphrey (1940, 26), in discussing whether or not ants can hear, cites chiefly the work of Autrum (1936, 24) whose experiments, according to Pumphrey, "...seem to show conclusively that the ants he studied (_Formica rufa_, _Myrmica_ spp., _Lasius_ spp.) are deaf to their own stridulations, but may respond to very loud artificial sounds." Pumphrey later says, "It would, therefore, seem very unlikely that air-borne sounds play any appreciable part in the perceptual field of the ant."

Other Orders

As can be readily seen, so little investigation has been done on the behavioral significance of insect sounds other than those made on some of the Orthoptera, that attempts to summarize or generalize with regard to function are little more than speculation in most cases. For the orders other than those mentioned above, the evidence is so slight that it is hardly worth considering in a discussion of function.

EQUIPMENT AND METHODS IN THE STUDY OF INSECT SOUNDS

Prior to the development of electronic sound recording and analyzing equipment, individual investigators were hard put to describe the differences they could hear in the sounds made by different species of insects. They usually attempted to give syllabic renditions of the sounds, portray them in terms of musical notations, or compare them to well-known sounds, such as tin whistles, Halloween rattles, etc. Such attempts have been largely unsuccessful because insect sounds are too unique and varied to be described in terms of other sounds that humans are used to hearing. It is an important fact, however, that these early workers could tell the sounds of different species apart by ear, in spite of the fact that they could not communicate their auditory impressions to others. Of all the sounds of the 130-odd species of insects recorded in the course of this study, there are probably less than a half dozen that cannot be immediately distinguished from all the rest by ear alone.

Nevertheless, when temporal parameters in insect sounds exceed ten or fifteen per second, we cannot count them, and when frequencies exceed 18-20 kilocycles per second, they are inaudible to humans. Both of these extremes are reached and far surpassed in many, if not most insect sounds, and in some the main part of the sound may be beyond our range of perception. The studies of Wever and Bray (1933, 26), and of Pumphrey (1936, 26) on the auditory organs of insects indicate that many of the characteristics of insect sounds which we cannot perceive by ear may be behaviorally significant as far as the insects are concerned. As yet, practically no work has been done to confirm this.

It is apparent that the analysis of insect sounds is not an "all or nothing at all" proposition. The better our instruments, the better (or more complete) will be our analysis, but we do not necessarily need "perfect" instruments, or instruments that will record and reproduce <u>every</u> part of the sound. Thus, the fact that such instruments have not yet been devised should not deter us from using those that are available. It is only important that we recognize the limitations of our equipment and do not attempt to carry our analysis further than these permit.

There are many different reasons for comparing insect sounds, and these may often determine what kind of equipment will be most useful. One investigator may want to find out what parts of the sounds are behaviorally significant, and how, and would therefore select the most accurate recording and reporducing equipment available, sacrificing all other attributes in favor of accuracy of reproduction. On the other hand, a taxonomist may have no more idea of the biological significance of a sound than he might have of the biological significance of slight differences in setal patterns or genitalic structures. Yet he can use such characteristics to separate species or establish phylogenetic relationships if he knows simply that he is comparing homologous structures, and that the differences he observes are real, and not due to temperature or some other variable in the environment. An individual interested in the taxonomic significance of insect sounds would be expected to sacrifice some accuracy or completeness of analysis in favor of the ability to obtain large numbers of recordings for comparative purposes. A physiologist may not even need to compare homologous sounds. He may be interested in the effect of some factor such as temperature, and needs only to know that the differences he observes are due to temperature and not to some other factor in the environment.

Thus, the equipment and methods most suitable for a particular investigation depend largely on the aims of the investigator, and what applications he wishes to make with his results, since no single instrument or set of instruments has yet been designed which will best suit the requirements of all types of investigations.

The History of Instrumental Analysis

Some very simple devices have been used by various investigators to increase their ability to count rapidly delivered temporal parameters in insect sounds. Fulton (1931, 6) was able to count as high as 8-9 pulses of sound per second by merely tapping the point of a pencil on a sheet of paper at the same speed as the pulse rate in the insect sound, and moving the pencil constantly so that he could later count the number of dots produced in a measured time. Later (1933a, 6) he employed a length of spring steel which could be set into vibration at a rate determined by the position of a sliding clamp. By locating this apparatus so that the end of the spring tapped against a revolving kymograph drum, and adjusting its speed of vibration to that of the insect's song, he could count pulsations up to 12 per second by counting the marks made in a measured period of time.

The first instrumental analysis of an insect sound was probably that performed by Kreidl and Regen (1905, 6) on the chirp of the European cricket, Gryllus campestris L. They used a stroboscopic device to determine the rate of wingstroke, and a phonograph recording on which they counted the marks to obtain the frequency of the sound.

Lutz and Hicks (1930, 6) performed "An Analysis by Movietone of a Cricket's Chirp (Gryllus assimilis)." They recorded the chirp of this cricket by means of a microphone which converted the sound waves to electrical energy and amplified the resultant currents to cause a "glow tube" to flicker in correspondence with the frequency and intensity of the sound. The glow tube was placed in a movie camera so as to expose a narrow strip beside the picture strip of the film.

Pierce (1948, 26) analyzed the sounds of 37 species of Orthoptera and 2 species of cicadas, using devices of his own design. The sounds were picked up by means of a sound-receiving unit employing a piezoelectric crystal mounted inside a parabolic, "sound-collecting" horn. This unit converted the sound waves to electrical energy and transferred the resultant current to a portable amplifier. The dominant frequency in the sound could be determined by setting a built-in, adjustable tuner to give a beat-frequency of zero with the incoming signal. The pulsations in the sound were recorded on a moving tape as deviations from a straight line. The stylus marking thus recorded the "modulation envelope," much as is done by modern oscillographs, and did not show the frequencies present in the sound.

Pielemeier (1946,26) utilized a sound level meter to determine the relative intensities of the frequencies present in the sounds of five species of Orthoptera, and a stroboscope to count the speed of wing motion during song.

Busnel and his associates at the Laboratory of Acoustical Physiology of the National Institute for Agricultural Research in Jucy-en-Josas, France, have at their disposal perhaps the most accurate combination of equipment ever used for the study of insect sounds. This includes a magnetic tape recorder which operates at a tape speed of 154 cm. per second, electrostatic microphones and amplifiers, and an oscillograph and a frequency analyzer. Their oscillograph portrays time on the horizontal axis and intensities on the vertical axis, thus giving a picture of the modulation envelope, and by exaggerating the time element, of the individual sound cycles in a sound of relatively pure frequency. One advantage of this machine over the Vibralyzer used in this study is that it gives a quantitative comparison of relative intensities with time. Their frequency analyzer portrays frequencies on one axis and relative intensities on the other at a selected place in the sound.

Equipment and Techniques Used in This Study

The following instruments have been utilized in the present study:

Microphones

1. BA-106, crystal (Brush Development Company, Cleveland 14, Ohio).

2. D-33 and D-33A, electrodynamic (American Microphone Company, 370 South Fair Oaks Avenue, Pasadena 1, California).

Magnetic Tape Recorders

1. Magnecorder PT3A2H with Magnecorder PT63J recording and playback amplifier (Magnecord, Inc., 360 North Michigan Avenue, Chicago 1, Illinois).

2. Magnemite, portable, Models 610-E and 610-EV (Amplifier Corporation of America, New York). Both of these units are operated by a spring motor, and have battery-operated recording units.

Audiospectrographs

Two different Vibralyzers (Kay Electric Company, Pinebrook, New Jersey) were used in the course of the study. One of these instruments belonged to the United States Air Force, and was used through the courtesy of Dr. Allen J. Hynek of the Department of Physics and Astronomy of the Ohio State University. The other was purchased by the Department of Zoology and Entomology in January, 1956, by means of a grant from the Ohio State University Development Fund.

Miscellaneous

1. Variable band-pass filter, Model 310-AB (Krohn-Hite

Instrument Company, Cambridge 39, Massachusetts).

2. Audio-oscillator, Model 200A (Hewlett-Packard Company, 395 Page Mill Road, Palo Alto, California).

3. Aluminum parabolic reflector, 24 inches in diameter.

Part of this equipment was originally obtained for use in studies on bird songs begun by Dr. Donald J. Borror and Dr. Carl R. Reese in 1948 and 1949. Tape and other miscellaneous supplies, in addition to the equipment listed above, were made available through funds appropriated by the Graduate School of the Ohio State University, The Ohio State University Development Fund, and the Department of Zoology and Entomology.

The procedure employed has been to first record the sounds, either in the field with one of the portable Magnemites, and usually with the microphone faced into a parabolic reflector (Plates VII, VIII), or in the laboratory in a cage or culture jar, with the Magnecorder (Plate VIII, Fig. 27). The tapes thus obtained were then edited, classified as to date, time, temperature, locality, situation, and species, given an identifying number and stored for later analysis. The insects recorded were captured when possible and labelled so that they could be identified with a given recording.

The first step in analysis of recordings consisted of playing them back at reduced tape speeds and timing chirp rates, pulse rates, counting the number of pulses per chirp, etc. Then audiospectrographs or <u>Vibragrams</u> were made at selected points in the tape and using different settings of the machines until the analysis had been carried

PLATE VII. RECORDING IN THE FIELD WITH MAGNEMITE AND PARABOLA

Fig. 25

PLATE VIII. RECORDING INSECTS WHICH PRODUCE SOFT SOUNDS

Fig. 26. Recording a ground cricket (Nemobius sp.) at close range in the field with microphone inside funnel.

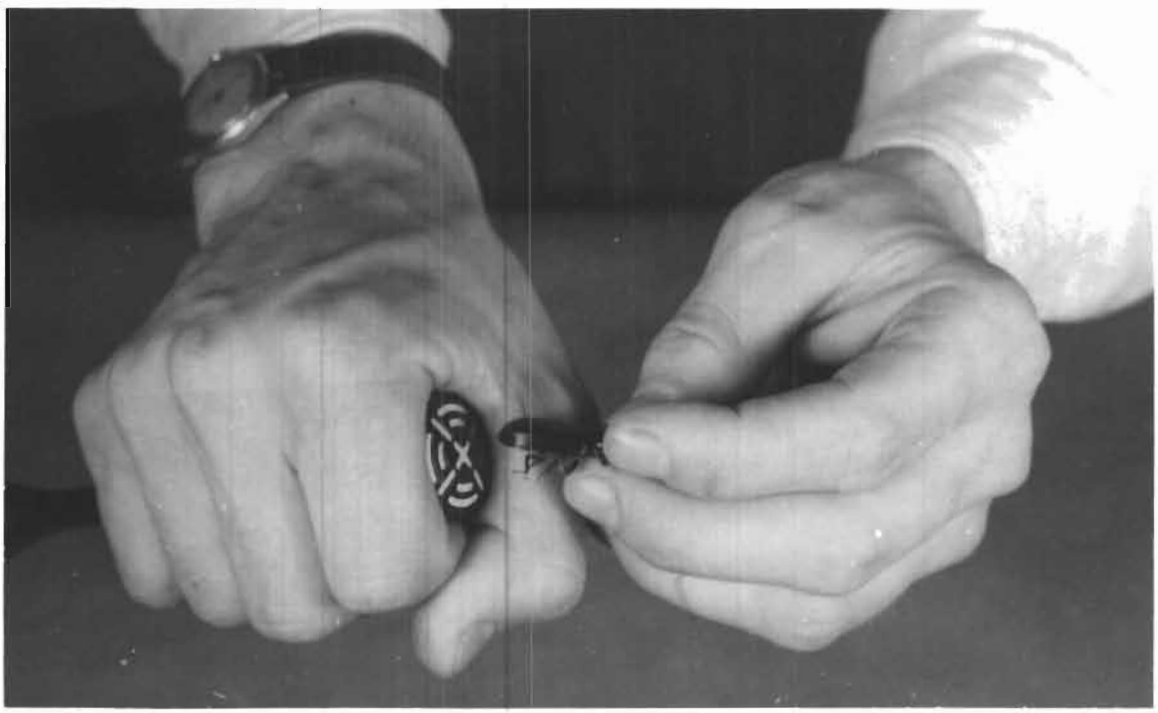


Fig. 27. Recording the "protest" sound of Popilius disjunctus (Illig.)(Coleoptera: Passalidae) in the laboratory.

as far as desired.

Two types of graphs, or Vibragrams, can be obtained with the Vibralyzer (Plates IX-XI). One type (chiefly used in this study) portrays time on the horizontal axis, frequencies on the vertical axis, and relative intensities by the darkness of the pattern. A second type (Section Vibragram) portrays relative intensities on the horizontal axis and frequencies on the vertical axis for any selected moment (actually integrated over 0.005 second) in the sound. Thus, the first type of graph (Regular Vibragram) allows quantitative comparisons of time and frequency elements, and gives a qualitative indication of relative intensities; the second type (Section Vibragram) allows quantitative comparisons of the relative intensities of different frequency elements at a given time. The first type of Vibragram yields a "three-dimensional" sound picture which is so meaningful that with a little practice, accurate predictions or "audio-visualizations" of what a graphed signal will sound like, can be made, although the sound has actually never been heard. Plate XI shows the relationships between the different kinds of sound pictures being used today to analyze and portray insect sounds.

Vibragrams are made on 5 5/8-by 12 3/4-inch dry facsimile paper, and occur as dark gray or black marks on a background of light gray. Frequencies are portrayed over a vertical distance of about four inches, and time over a horizontal distance of about 12 1/2 inches. The paper is fastened to a drum which rotates synchronously with the magnetic disc bearing the signal to be analyzed. It is marked by a

PLATE IX. THE VIBRALYZER (Fig. 28)

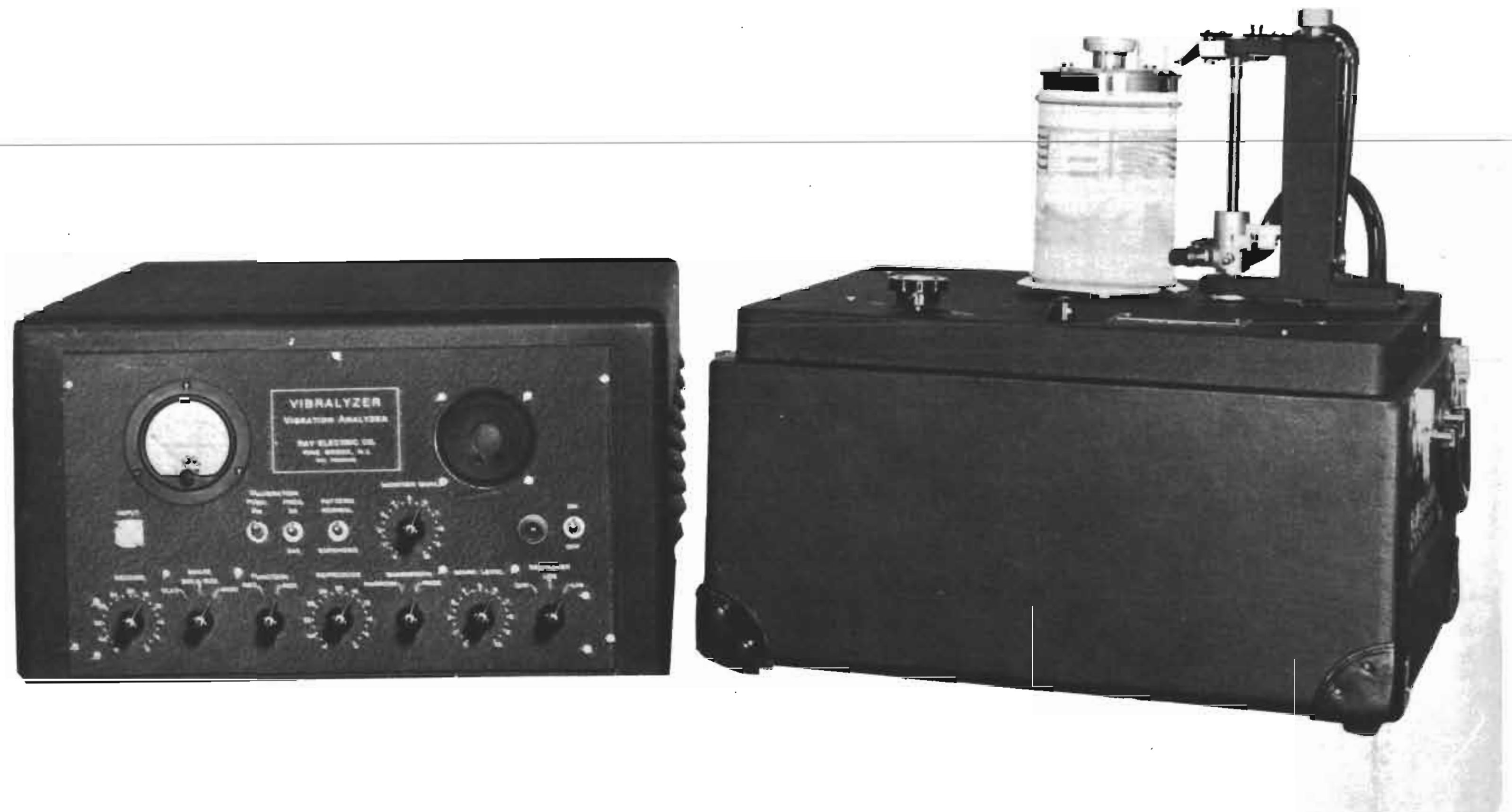


PLATE X. CIRCUITS OF THE VIBRALYZER (Fig. 29)

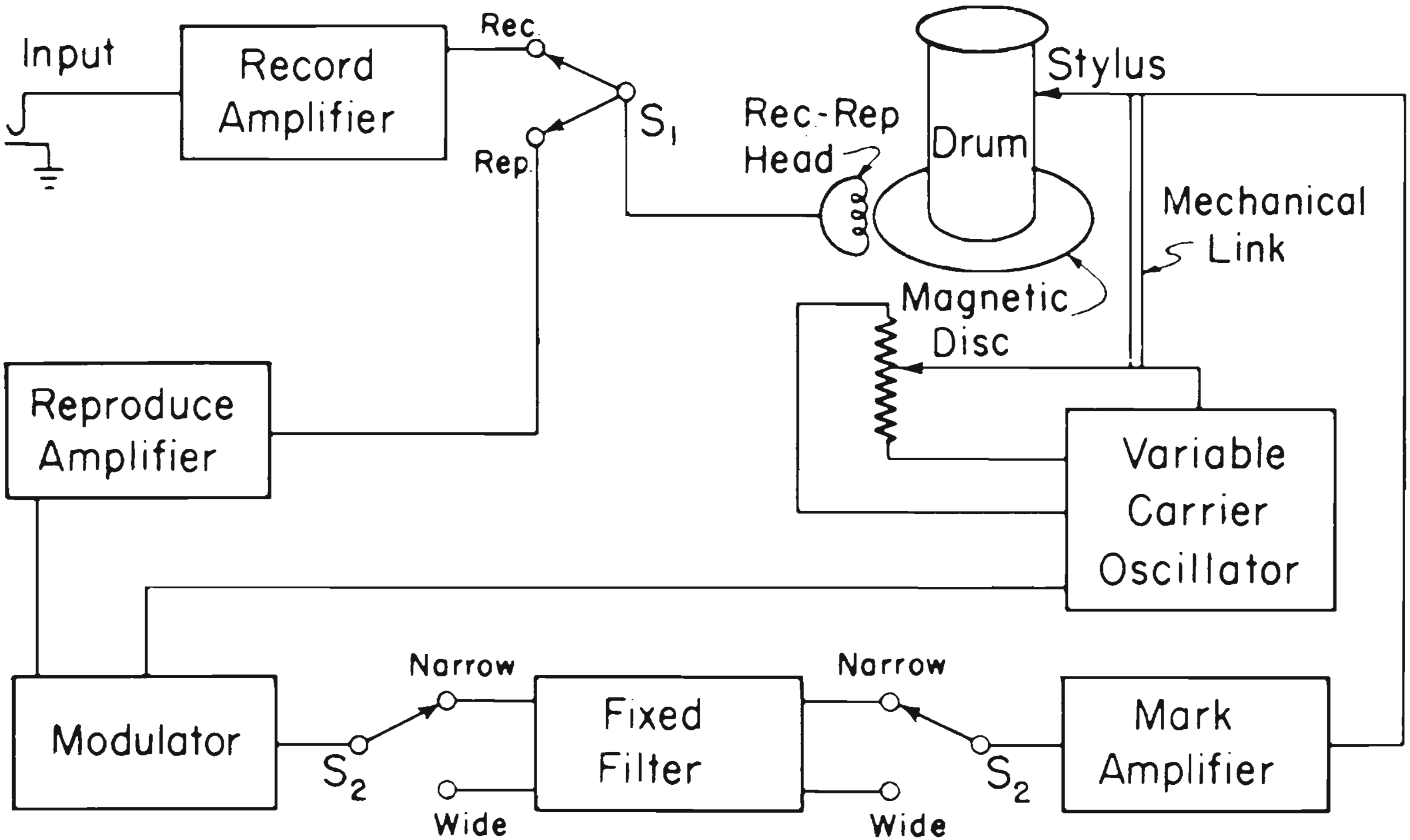
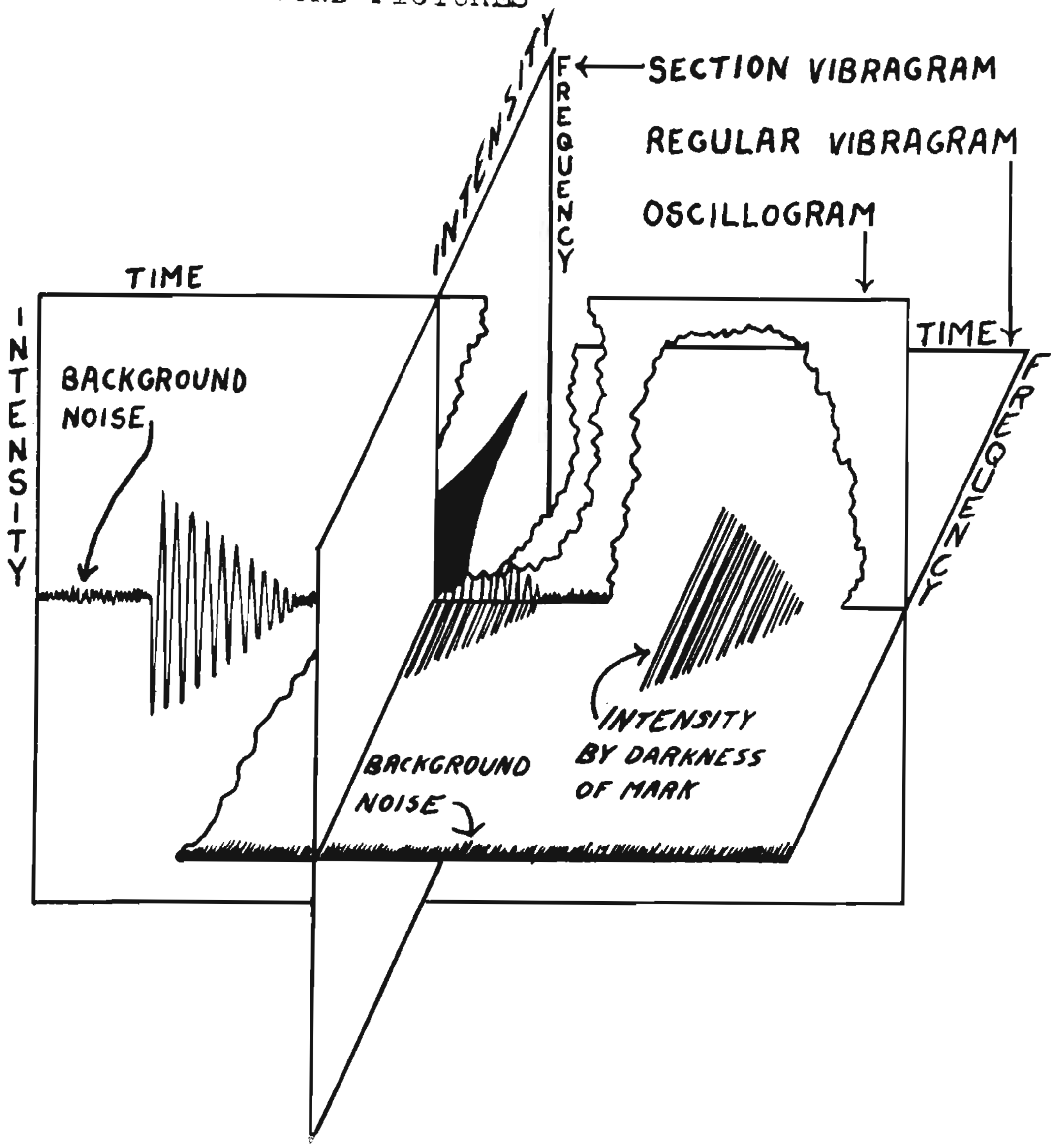


PLATE XI. RELATIONSHIPS OF DIFFERENT TYPES OF SOUND PICTURES
(Fig. 30)



A hypothetical 3-pulse (3- wingstroke) cricket chirp dominated by a pure frequency, each pulse with 11 tooth-strikes (each toothstrike corresponding to one cps.)

10 mil stainless steel stylus in terms of horizontal lines, 1/96 inch apart.

A simplified diagram of the principal circuits of the Vibralyzer is shown in Plate X. The input signal (from a tape recording of the sound) is recorded on a magnetic disc (with the switch S_1 in the "record" position) by means of a record amplifier. Once the desired signal is on the disc, S_1 is turned to the "reproduce" position. The signal on the disc may be heard by means of a monitor amplifier (not shown on the diagram) each time the disc rotates. When the Vibragram is made, the disc is rotated at a speed of 80 revolutions per minute, the signal is played back from the disc by means of a reproduce amplifier, and the output of this amplifier is fed into a modulator which modulates the playback signal with the output of a variable carrier oscillator. The frequency of this oscillator is determined by the position of the stylus, through a mechanical linkage. The modulated signal is fed to a fixed frequency filter, and the output of the filter actuates the mark amplifier which in turn supplies a marking voltage to the stylus. As the Vibragram is made the stylus moves upward on the drum, causing the oscillator to sweep through its frequency range and thus effectively scan the recorded signal over this range. The frequency of the oscillator at any given position of the stylus determines what frequencies in the recorded signal will give rise to a difference frequency that passes through the filter and results in a mark by the stylus.

The filter is set for a frequency of 15, 000 cycles per second, and the carrier oscillator frequencies vary from 15,133 to 28,300; thus the reproduced frequency range is from 133 to 13,300 cycles per second. The frequency range covered in any Vibragram can be changed by varying the playback speed of the tape, or the speed of the magnetic disc when the signal is being transferred. The Magnecorder can be played at three different speeds (15, 7½, and 3 3/4 inches per second), and the disc on the Vibralyzer can be rotated at four different speeds. Thus, the following frequency- and time-range combinations can be obtained on Vibragrams without re-recording the sounds at different tape speeds.

Table 1

Frequency- and Time-Range Combinations Available on Vibragrams

Frequency Range of Vibragram in Cycles per second	Effective Band Width in Cycles per Second		Approximate Duration of Signal in Cycles per Second
	Narrow	Wide	
5 - 500	2	20	20.0
10 - 1000	4	40	10.0
15 - 1500	6	60	6.6
20 - 2000	8	80	5.0
30 - 3000	12	120	3.3
44 - 4400	20	200	2.4
60 - 6000	24	240	1.65
88 - 8800	40	400	1.2
133 - 13,300	64	640	0.75
176 - 17,600	80	800	0.6
266 - 26,600	128	1280	0.375
532 - 53,200	256	2560	0.1875

Only the wide band width was used in the Vibragrams portrayed in this paper, since this allowed a more accurate reading of the time element, considered to be of greater importance than the exact frequencies. The settings utilized for a particular sound depend on its characteristics and must be determined by trial and error to obtain the best results. Time elements can be read more accurately as the tape speed is reduced and the disc speed increased during transference of the signal, but frequency determinations become correspondingly less accurate. Also, as the time element is exaggerated, the pattern drops toward the bottom of the graph. The frequency range can be reduced to one-half at any setting by moving a switch on the control panel, thus moving the frequencies up from the botton of the paper without sacrificing ability to accurately read time elements.

Most insect sounds are relatively high-pitched, and contain high-speed intensity modulations or pulsations. Thus they are well-suited for analysis with the Vibralyzer, since they usually fall near the center of the graph when the time scale is exaggerated, making the individual pulsations distinct. Also, most background noise is low-pitched, and thus appears along the bottom of the graph at settings which best portray insect sounds. Thus a very "dirty" recording, on which the insect sound can scarcely be heard at all, can be successfully analyzed on the Vibralyzer, and often a very clean Vibragram can be reproduced from such recordings. Usually, when the insect sounds in the Vibragrams used in the figures in this paper seem to pass off the bottom of the graph, this part has been removed because excessive background noise completely obscured the insect sound below this point.

Measurements of frequency on the Vibragrams were made with scales prepared by passing audio-oscillator notes through the same steps in recording and tape speed reduction as those passed through by recordings of insect sounds. Time scales were prepared by timing the speed of revolution of the Vibralyzer drum and dividing the functional length of the graph paper into units corresponding to tenths of seconds. Both scales were checked at frequent intervals and adjusted to compensate for small changes which appeared from time to time in the speed of revolution of the Vibralyzer drum and the position of frequencies on the Vibragram, due to stylus adjustments, etc.

The equipment described above is not considered ideal for the study of insect sounds, but it is believed to be the best available for the type of study conducted. The crystal microphone was not suitable since it had a peak response at around 4 kilocycles per second, and a rapid drop-off above 6 kilocycles per second. For this reason it was discarded as soon as the electrodynamic microphones could be utilized. With the D33A microphone, used almost exclusively during 1955, the equipment can be considered to perform with fair consistency up to 15 kilocycles per second, according to the manufacturers' specifications. The chief weaknesses below this extreme lie in the possibility of deviations from flatness of frequency response. Practically no emphasis has been placed on the structure of the frequency spectrum in the multi-frequency sounds encountered in this study, and nothing is said concerning pulsations occurring at rates faster than two or three hundred per second. To accurately record higher frequencies, a tape speed higher than 15 inches per second would have been necessary, and this is not available in portable recording equipment. If taxonomic applications are to be made, the number of individual recordings necessary could not possibly be made in the laboratory or with non-portable equipment. In spite of the demonstrations by other workers, such as Pielemeier (1946, 6), Pierce (1948, 26) and Busnel (1953, 6) of frequencies as high as 60-100 kilocycles per second in insect sounds, there is no evidence that any insect produces a sound with supersonic components and no sonic components. In fact, it seems apparent that the majority of insect sounds have their most intense components within the sonic range. All of the known cricket sounds, which are characterised by an almost pure dominant frequency, have this most intense frequency below ten kilocycles per second. The investigations of Wever and Bray (1933, 26), Pumphrey and Rawdon-Smith (1936, 26), and Regen (1913, 6) indicate that changes in pitch or differences in the frequency spectra of the sound pulses of insect sounds are scarcely or not at all behaviorally significant. Consequently it does not seem necessary to postpone studies of insect sounds until equipment capable of accurately recording and portraying <u>all</u> the frequencies present and their relative intensities has been designed.

Problems in Recording Insect Sounds

Due to the diversity of situations in which insects make their various noises, and the tremendous range of frequencies and intensi -

ties encountered in the sounds of different species, a variety of techniques must be employed to obtain satisfactory recordings, each suited to a particular insect or group of insects. Some insects must be recorded in the field, and other must be recorded in the laboratory. Some insect sounds are so soft that they must be recorded in special sound-proof chambers to reduce background noise; others are intense, and loud enough to carry a half mile or more for human ears. Special conditions are often necessary to elicit sound production from an insect. Many Orthoptera sing only at night; some cicadas sing less than an hour each day. Although many species produce their sounds rather continuously under favorable conditions, others may produce a brief note at wide or irregular intervals, and move from one location to another between songs, thus making it very difficult to get their song recorded. I have spent several hours in the hemlock forest at Ash Cave in Hocking County, Ohio, when the night air was filled with the soft lisps of the hemlock bush katydid, *Scudderia fasciata* Beutenmuller, and have come away without a single suitable recording of the species. Often the only recording obtained of such a species has been gotten by simply aiming the parabolic reflector into the woods containing the insects and allowing several reels of tape to run through the recorder while sweeping the reflector in a slow arc, hoping that it will, by chance, be aimed at some individual when it sings. Sometimes a recording is made and the insect that produced it cannot be captured for identification. I still have several unidentified recordings. In some cases, such as with <u>Hubbellia marginifera</u> (Walker), which sings from 20, 30, or 40 feet high in pine trees in North Carolina, several hours were spent searching out specimens and then climbing trees to capture them, after spending less than five minutes making the actual recording. In cases such as these, the task of getting enough recordings of enough captured specimens to use the results in a taxonomic investigation often seems hopeless.

One of the biggest problems in field recording is the elimination of extraneous noises. The high noise level of our civilization is quickly brought home to anyone who attempts to make field recordings of insect sounds. To complicate the issue, there may often be dozens of species and hundreds or even thousands of individuals singing in a relatively small area, making the singling out of the song of one individual a practical impossibility.

In general, field recordings were made with the microphone faced into a parabolic reflector as shown in Plate VII. However, early in the season when only a few species are singing, this was not necessary, and the microphone was used alone, or simply placed inside a funnel of cardboard or metal covered with electrician's tape, as shown in Plate VIII, Figure 26. In all cases the microphone was placed as near to the insect as possible. In the laboratory the microphone was generally only a few inches away, while in the field it may have been only a few inches away, or many yards, depending on the insect, its wariness, and the height and location of its singing perch.

Bringing insects into the laboratory to record their sounds presents a number of problems. Unless the specimens are caged individually they may eat each other before they ever get into the laboratory, or at least damage or destroy each other's sound-producing organs. If extended field trips are made, rather cumbersome rearing jars and cages must be carried along to insure that the specimens can be brought back alive and healthy. Some insects, such as the cicadas, do not sing when caged in the laboratory, and others are apparently only partially stimulated, and the sounds that they produce in the laboratory may not be at all typical of what is produced in the field. It may take several days of watching to catch a caged insect singing, and often the microphone and cord must be left in place by the cage during this time to avoid disturbing the insect by setting up the equipment after it has started to sing.

Care must be taken when recording in the laboratory to have the insect in a container which does not reverberate. Glass jars and plastic rearing dishes are not very satisfactory.

Whether a recording is made in the field or in the laboratory, the temperature should be taken as near the insect as possible at the time of recording. All insect sounds are delivered more slowly as the temperature drops; two species may have different songs at the same temperature, but their songs may be exactly alike if recorded at temperatures differing by only ten or fifteen degrees Fahrenheit. Recordings of insect sounds in which the temperature is not recorded are worthless for most comparative purposes. In the field, temperatures may vary as much as ten to fifteen degrees Fahrenheit in spots only a few yards apart.

When time and circumstances allowed, each of the insects studied was observed in as many different situations as could be imagined and produced in which it might make a sound. In many beetles, mutillids, bugs, and others, the "protest" sound was the only recording obtained. In most of these it is the only sound known. In others, such as the Orthoptera, males were confined alone at times, and with males and females of their own species at other times. Sometimes it was necessary to place the cages in a dark room; in other cases the recordings were made in daylight. In every case the exact conditions, so far as they can be described, are given in the write-ups on individual species.

THE EFFECT OF TEMPERATURE ON INSECT SOUNDS

A great many questions have arisen since Dolbear (1897, 6) devised his now famous formula which stated, in effect, that in the song of the snowy tree cricket, the number of chirps in fifteen seconds plus forty gives an approximation of the temperature in degrees Fahrenheit. Various authors have confirmed (Faxon, see Edes, 1899, 6) or disagreed somewhat (Bessey, 1898, 6; Edes, 1899, 6; Shull, 1907, 6) with Dolbear's results, and others have demonstrated rate change with temperature in the songs of other species of Tettigoniidae and Gryllidae (Fulton, 1931, 1933, 6, several species of Nemobius; Pierce, 1948, 26, Nemobius fasciatus (DeGeer)). Fulton (1925, 6) pointed out that physiological variation could possibly be involved in the difference in results obtained by investigators working with the snowy tree cricket in different parts of the country. He found two forms in Oregon which differed from each other in chirp rate, among other things, and which he termed "physiological races."

More recently, R. G. Busnel and M. C. Busnel, working with the European tree cricket, Oecanthus pellucens Scop., have indicated that they could observe no change in this insect's song across a temperature range of 12-35°C. (personal communication). They state that the dominant frequency in the song of O. pellucens corresponds to the number of teeth struck per second, and that no change in frequency with temperature has been observed. This would lead to the assumption that there is also no change in rate of wingstroke, unless only the speed of wing motion in the non-acoustic portion of the stroke changes with change in temperature.

H. Frings (paper presented at the 1955 Entomological Society of America Meetings), on the other hand, found a logarithmic relationship between temperature change and change in the rate of wingstroke in the song of Neoconocephalus ensiger (Harris).

Chadwick (in Roeder, 1953, 26) points out that the effects of temperature change on the wingbeat frequency of insects in flight are somewhat more complex than had been previously suspected. He notes that various factors such as humidity, age of the insect, fatigue, and a difference between the body temperature of the insect and the air temperature may have effects on the wingbeat frequency in flying insects. Chadwick distinguishes three "types" of insects with respect to the effect of variations in air temperature on the wingbeat frequency in flight: (1) those in which wingbeat frequency is essentially independent of external temperature, exemplified by the Hymenoptera and the beetle Cantharis, (2) those in which temperature dependence is apparent at the extremes of the physiological range, but lacking at intermediate temperatures (Schistocerca), and (3) those in which a positive correlation of wingbeat frequency with temperature is obvious over the entire range at which flight occurs (Diptera and the moth Hemaris).

The effects of temperature on the rate of wingstroke in a few of the species involved in this study are shown in Plates XII-XIV. No experiments have been performed in which any factor other than temperature was controlled. The points plotted on the scatter diagrams represent different individuals recorded both in the labora-

PLATE XII. EFFECT OF TEMPERATURE ON RATE OF WINGSTROKE IN TETTIGONIID SONGS

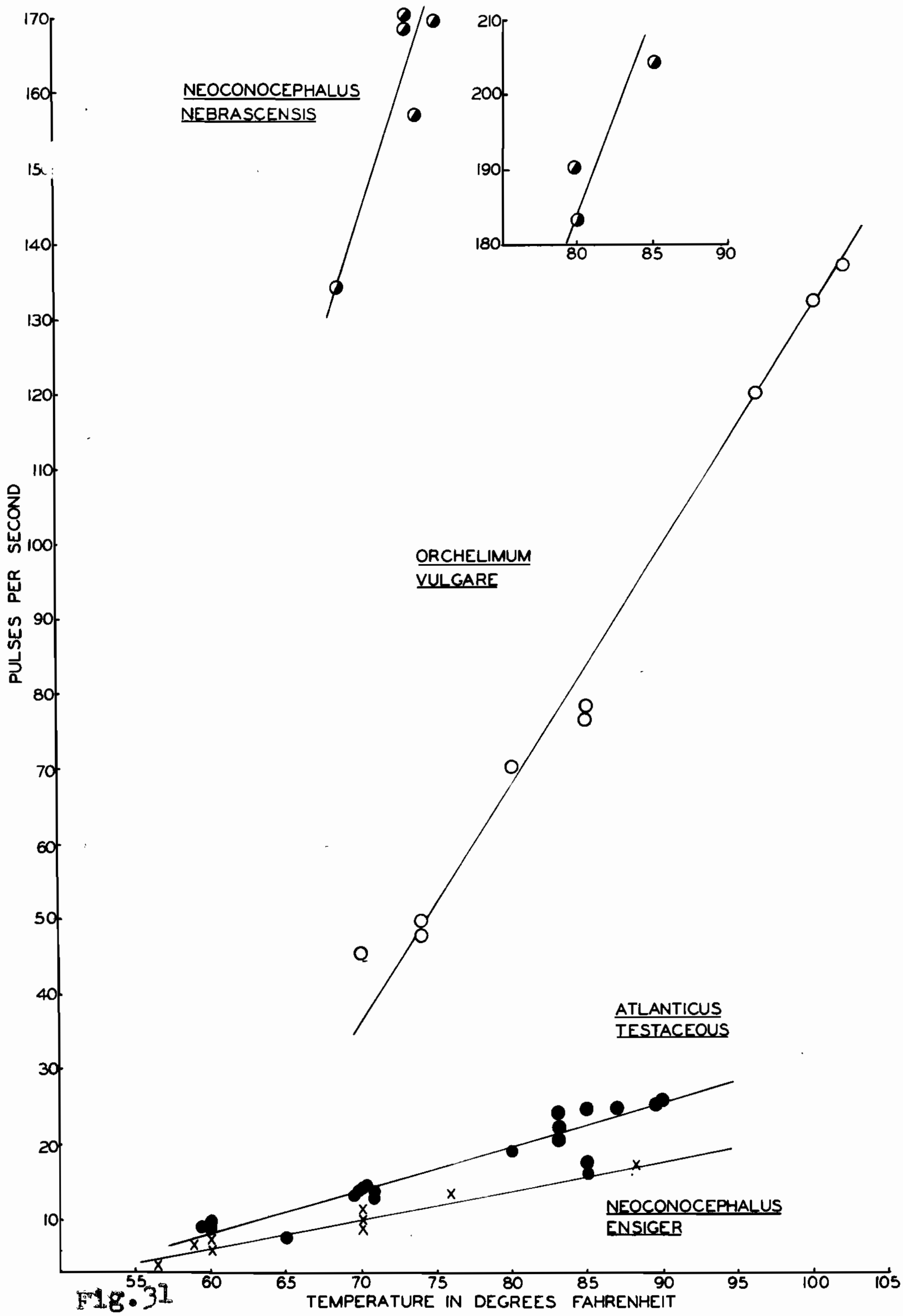


Fig. 31

PLATE XIII.

EFFECT OF TEMPERATURE ON RATE OF WINGSTROKE IN CRICKET SONGS

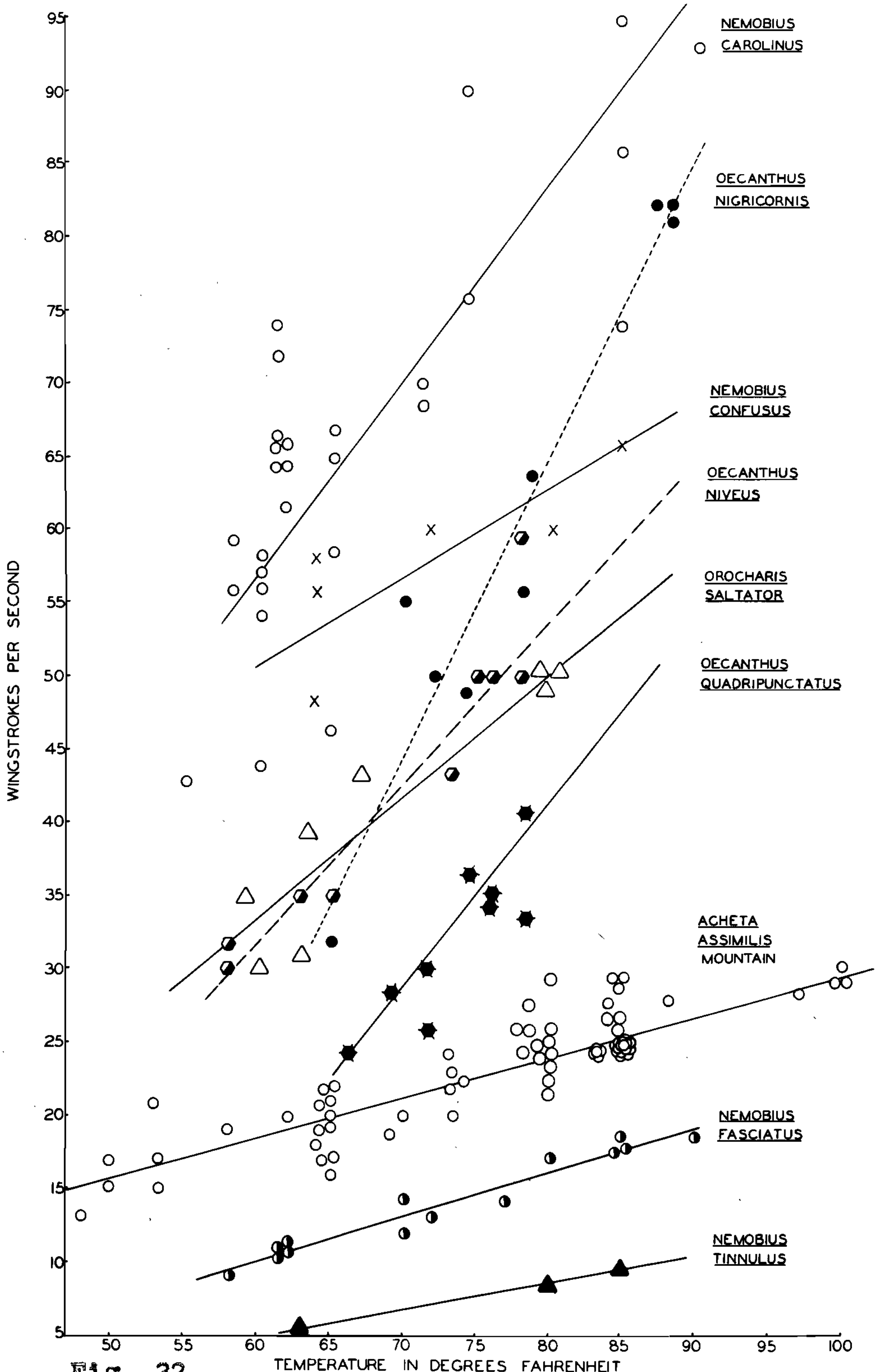


Fig. 32

PLATE XIV. CHANGE IN FREQUENCY IN CRICKET SONGS WITH CHANGE IN WINGSTROKE RATE

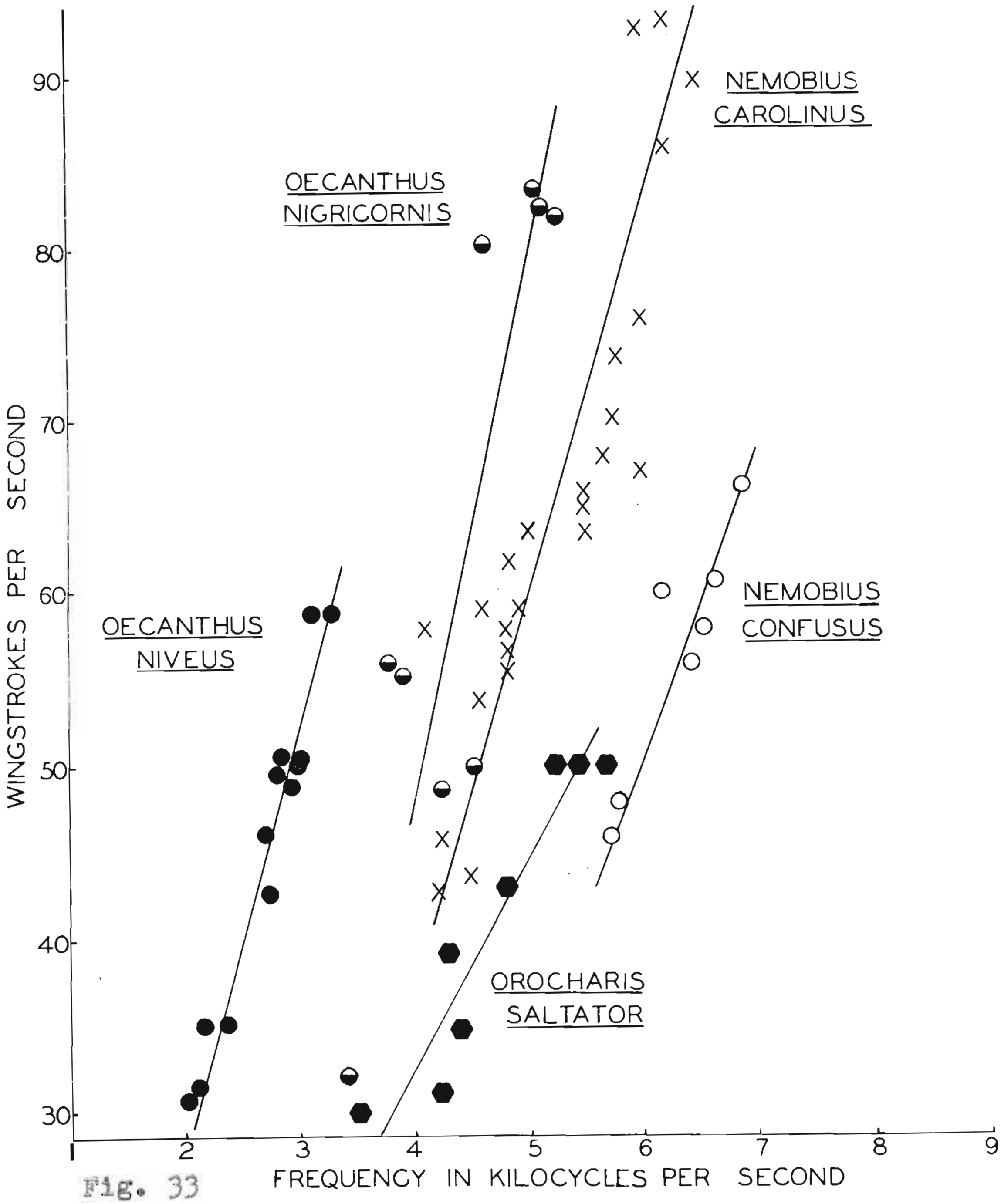


Fig. 33

tory and in the field, with the thermometer held as close to the singing insect as possible at the time of recording.

In spite of the wide range of variation at the same temperature in some cases, probably due in part to error in measurement of temperature, very little complexity exists in these data. All relationships appear to be linear or nearly so, with the possible exception of Nemobius carolinus, whose wingstroke rate seems to curve downward a little at the lower part of the temperature range. No logarithmic or temperature-independent characteristics are apparent, in spite of the wide variety of insects for which data are given, and the large number of observations in some cases. Seven genera in six different subfamilies are represented. Neoconocephalus ensiger, the same species which Frings found to show a logarithmic wingstroke rate change with temperature only a few hundred miles east of Ohio, definitely shows a straight line relationship, but the number of observations here are too scanty for adequate comparison. Three species of Oecanthus, the same genus studied by the Busnels in France, all show definite temperature dependency, both in wingstroke rate and frequency. In fact, the three species of Oecanthinae treated in Plate XIII, show a noticeably sharper increase in pulse rate with increase in temperature than do the Gryllinae plotted on the same diagram. Orocharis saltator, in the subfamily Eneopterinae, appears to be somewhat intermediate between these two groups.

It is noteworthy that the work of Fulton, Pierce, Bessey, Eades, and Shull (cited earlier) all show essentially linear relationships in the effect of temperature change on rate of chirp or wingstroke in the various species involved in their separate studies. The only deviation from this was in the work of Bessey who found that below 60°F., a slightly higher rate of wingstroke existed than would be expected by the formula based on a linear relationship.

A great deal more evidence for temperature dependency in rate of wingstroke, chirp rate, and frequency in a large number of species can be found in the data from individual recordings throughout the individual species write-ups in this paper. In short, every species which has been observed at two or more different temperatures shows a significant variation in song characters with temperature change, either in wingstroke rate, chirp rate, or in frequency. It seems unbelievable that the wide variation in response to temperature change reported by different investigators could exist in the same and closely related species. This aspect of the study of insect sounds certainly needs more investigation to clear up the seeming discrepencies.

As shown in Plate XXVI, temperature differences as slight as ten or fifteen degrees Fahrenheit may practically nullify the differences between the songs of different species of Acheta. This also is true in other species, in Oecanthus, Nemobius, and Scudderia. I have considered it necessary to record temperatures for every recording in which characters susceptible to temperature change are to be compared. Neither Pierce (1948, 26) nor Busnel and his associates in their many publications have recorded temperatures for specific recordings in such a way that this factor can be eliminated as a cause of the variations they have observed, or taken into account in comparing data with that given in their publications. This seems to be an omission of fundamental importance.

THE SINGING GRYLLIDAE, TETTIGONIIDAE, AND CICADIDAE

OF EASTERN UNITED STATES

Descriptions and Analyses of Songs and Singing Behavior, and Notes on Seasonal, Ecological, and Geographical Distribution

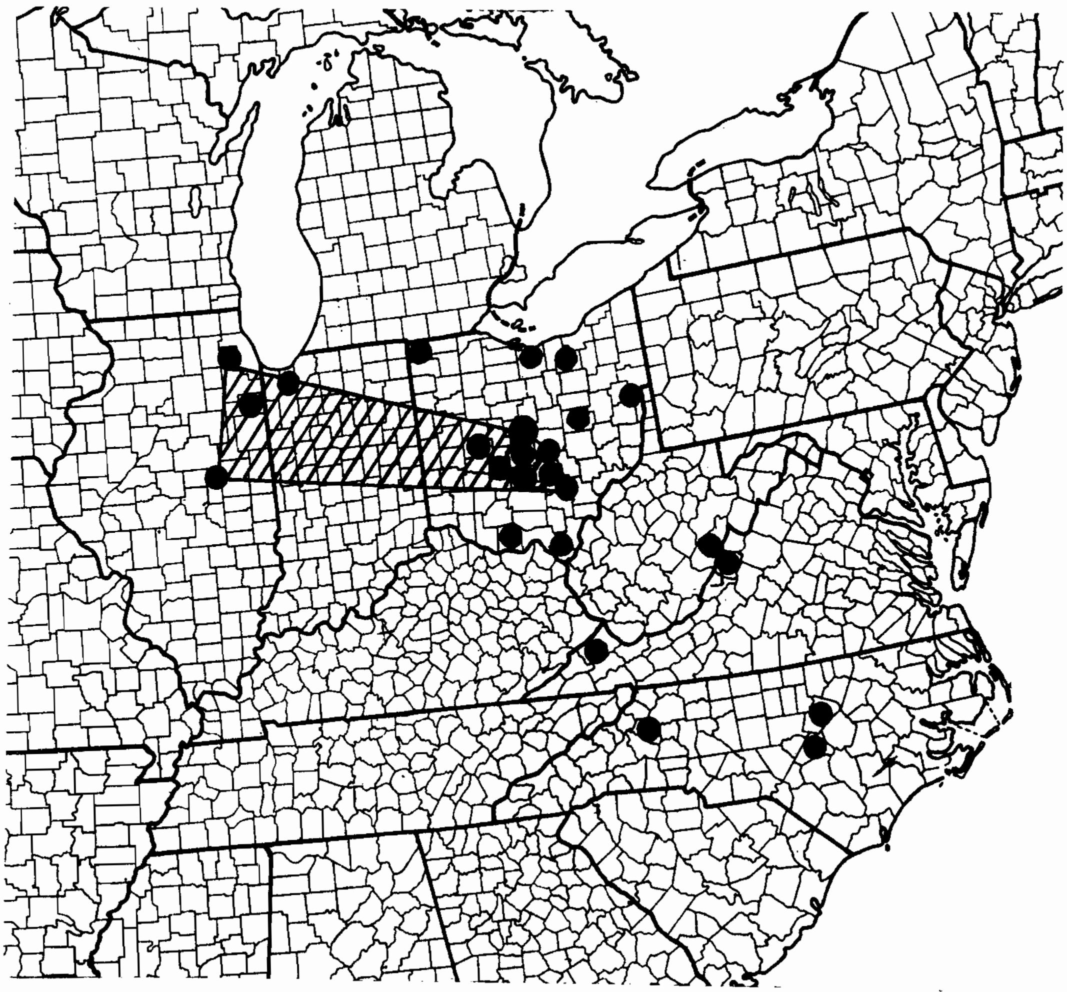
Introduction

The songs of 32 species of Gryllidae, 42 species of Tettigoniidae, and 11 species of Cicadidae have been recorded in the course of this study. This constitutes the majority of singing species found east of the Mississippi River in each of these groups.

Most of the work has been done in central Ohio. However, during the two seasons of the study, trips have been made all over the state of Ohio, several trips were made to central and northern Illinois, and a week-long trip was made to Raleigh, North Carolina. Plate XV shows the localities in which recordings were made, and the area in which observations were made over a considerable part of the singing season both years.

The amount of information gathered for the different species varies greatly. Some have been observed almost continuously for two seasons on and near the Ohio State University Campus at Columbus. Others have been recorded and observed at only one place and one time. Due to the fact that the field crickets in the genus Acheta were my chief interest when I began this study, the information given for this group is particularly detailed and complete, and written up in a somewhat different manner than that given for the rest of the

PLATE XV. GENERAL AREA COVERED IN THIS STUDY



The black dots are recording stations. Those inside the hatched area were visited several times during the singing seasons; others were visited only once or a few times during the two years.

Fig. 34

species. Except for this group an attempt has been made at uniformity of style.

All the information I have been able to gather concerning song, singing behavior, ecology, life history, and any peculiarities of distribution is given for each species. The appearance in several groups of variously distinct "song forms," in some cases distinct species, in others, some sort of infraspecific populations, has prompted a rather thorough survey of the literature to detect any results which might differ significantly from those given here. Due to the tremendous number of casual notes on singing Orthoptera, a complete literature survey could not be made in the time available. However, it is believed that most of the important papers have been seen, and all observations which were complete enough to compare with those given here are mentioned.

As shown in Plates XVI-XVII, most of the Gryllidae, Tettigoniidae, and Acrididae, sing from early July to late September in eastern United States (see also Cantrall, 1943, 6, p. 59-66; Fulton, 1951, 6). Most have but one generation per year. A few, such as Neoconocephalus triops (Fulton, 1951, 6), Chortophaga viridifasciata, and several species of field crickets, overwinter as adults or late instar nymphs, and begin to sing in April or May. Some species, such as Oecanthus latipennis, do not mature till sometime in August and are apparently largely killed off by frost. Others, such as Orchelimum gladiator, begin singing in early July and are gone a month or so before the first frosts. A few species, such as the

PLATE XVI. SONG RECORDS FOR GRYLLIDAE AND CICADIDAE IN CENTRAL OHIO

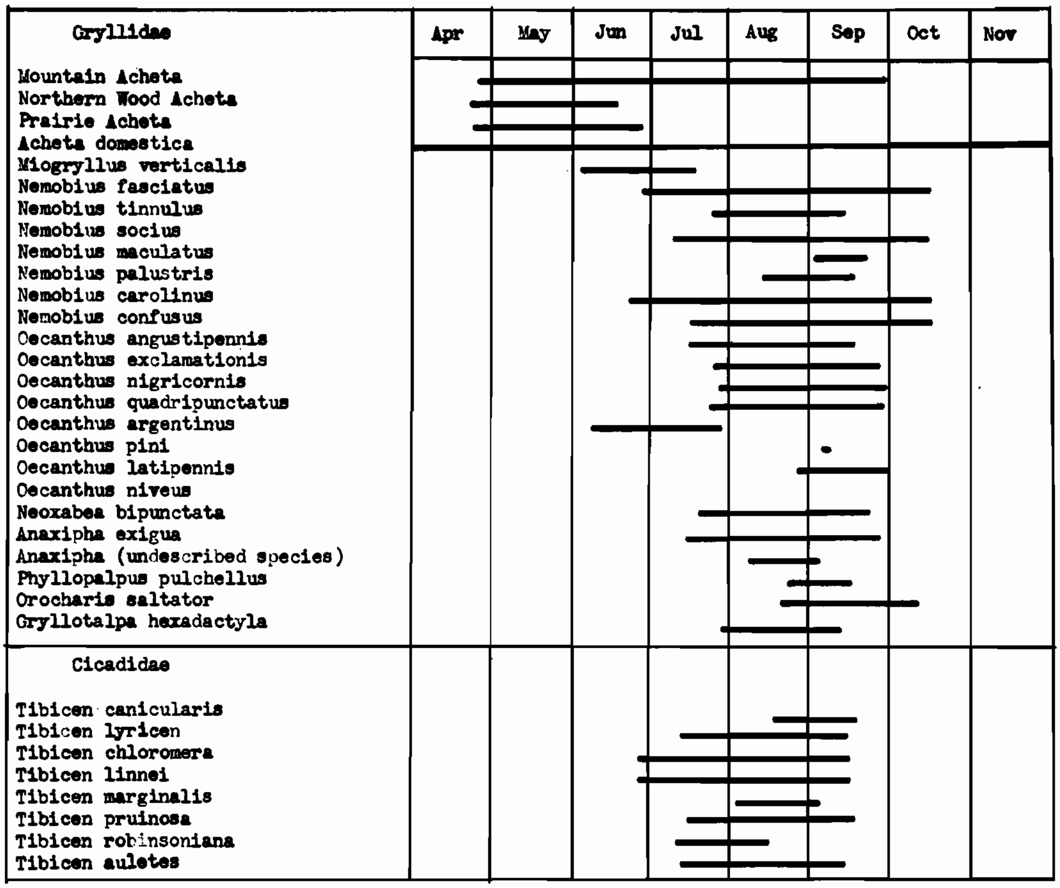


Fig. 35

PLATE XVII. SONG RECORDS FOR TETTIGONIIDAE AND ACRIDIDAE IN CENTRAL OHIO

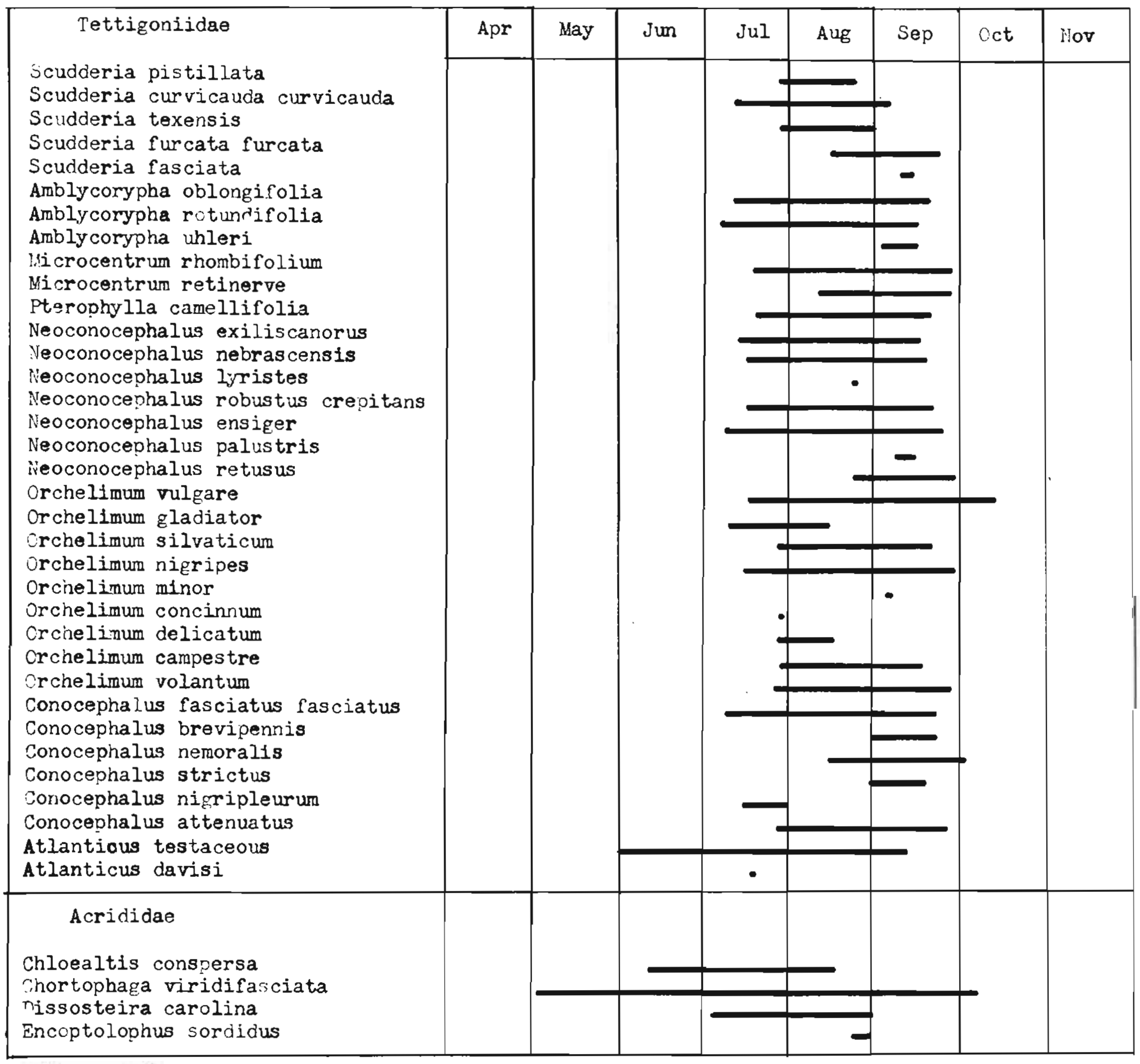


Fig. 36

triller Acheta (Fulton, 1952, 6) and probably Nemobius carolinus, have two generations per year. Some species, such as Gryllotalpa hexadactyla (see Fulton, 1951, 6) may have a two-year life cycle. Hancock (1916, 26) was unable to get eggs of Amblycorypha oblongifolia to hatch in less than two or three years.

All of the singing Gryllidae and Tettigoniidae in eastern United States, as shown on Plates XVIII-XIX, are either night-singers, or sing both day and night. Some species, such as certain Acheta and Oecanthus sing much more at night than in the daytime, but sing sporadically all during the day. According to Scudder (1868, 6) and Cantrall (1943, 6), the Scudderia sing differently by day than they do at night. I have found that Orchelimum vulgare and O. gladiator usually leave out the ticking part of their song at night.

Busnel (personal communication) indicates that the European orthopteran, Ephippiger bitterensis, sings only during certain hours of the morning. The Acrididae and the Cicadidae are the chief day-time singers in the United States, with some of the Cicadidae singing mostly in the morning (Tibicen chloromera), others chiefly in the afternoon (T. linnei), and still others only for a short period at dusk in the evening (T. auletes and T. resonans). The daily song period of the cicadas usually overlaps in the evening with the nightly song period of the Orthoptera. Many of the loud, night-singing Orthoptera stop singing shortly after midnight or one in the morning, and long before dawn the air has again become dominated by the softer sounds of those species which continue to sing in daylight.

PLATE XVIII. DAILY SONG PERIODS OF OHIO GRYLLIDAE AND CICADIDAE

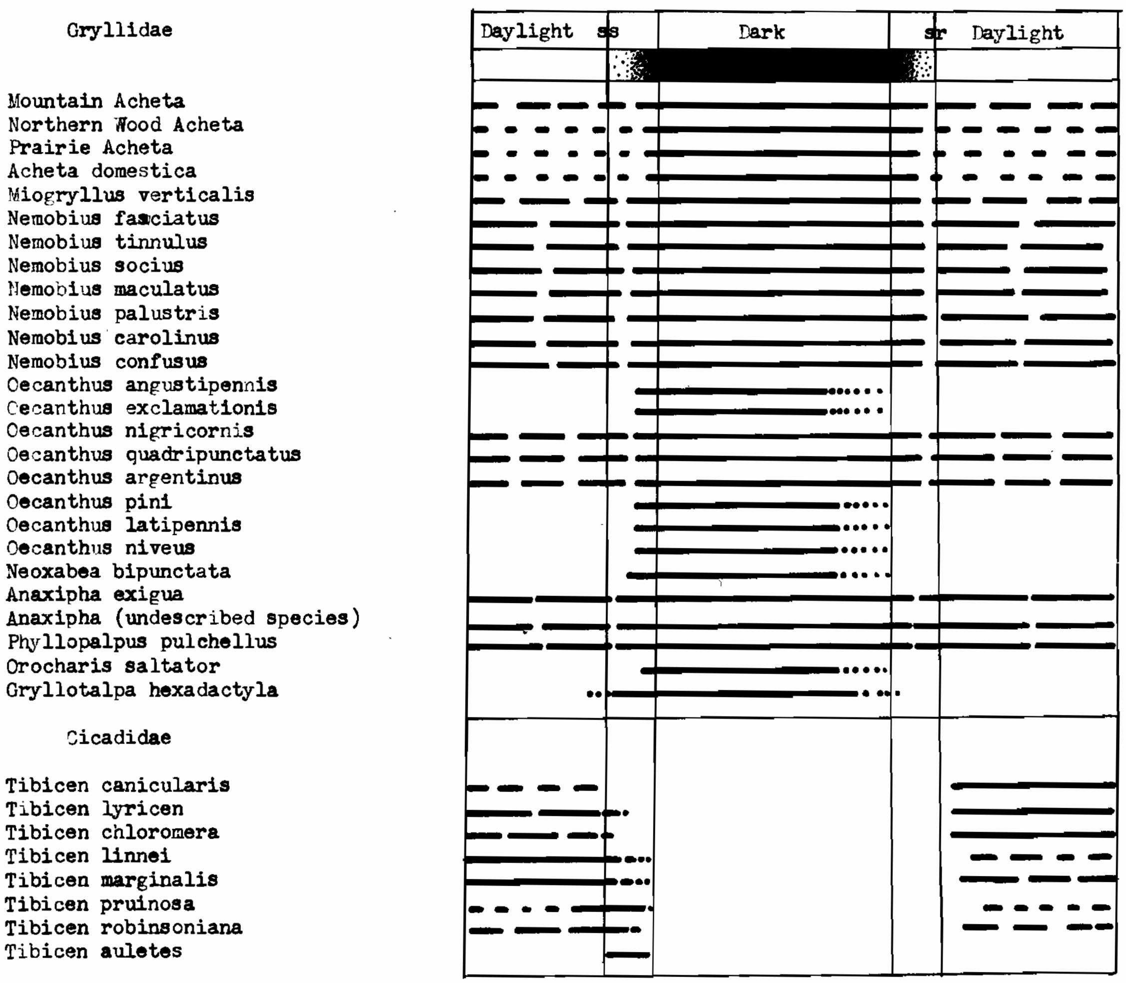


Fig. 37

PLATE XXIX. DAILY SONG PERIODS OF OHIO TETTIGONIIDAE AND ACRIDIDAE

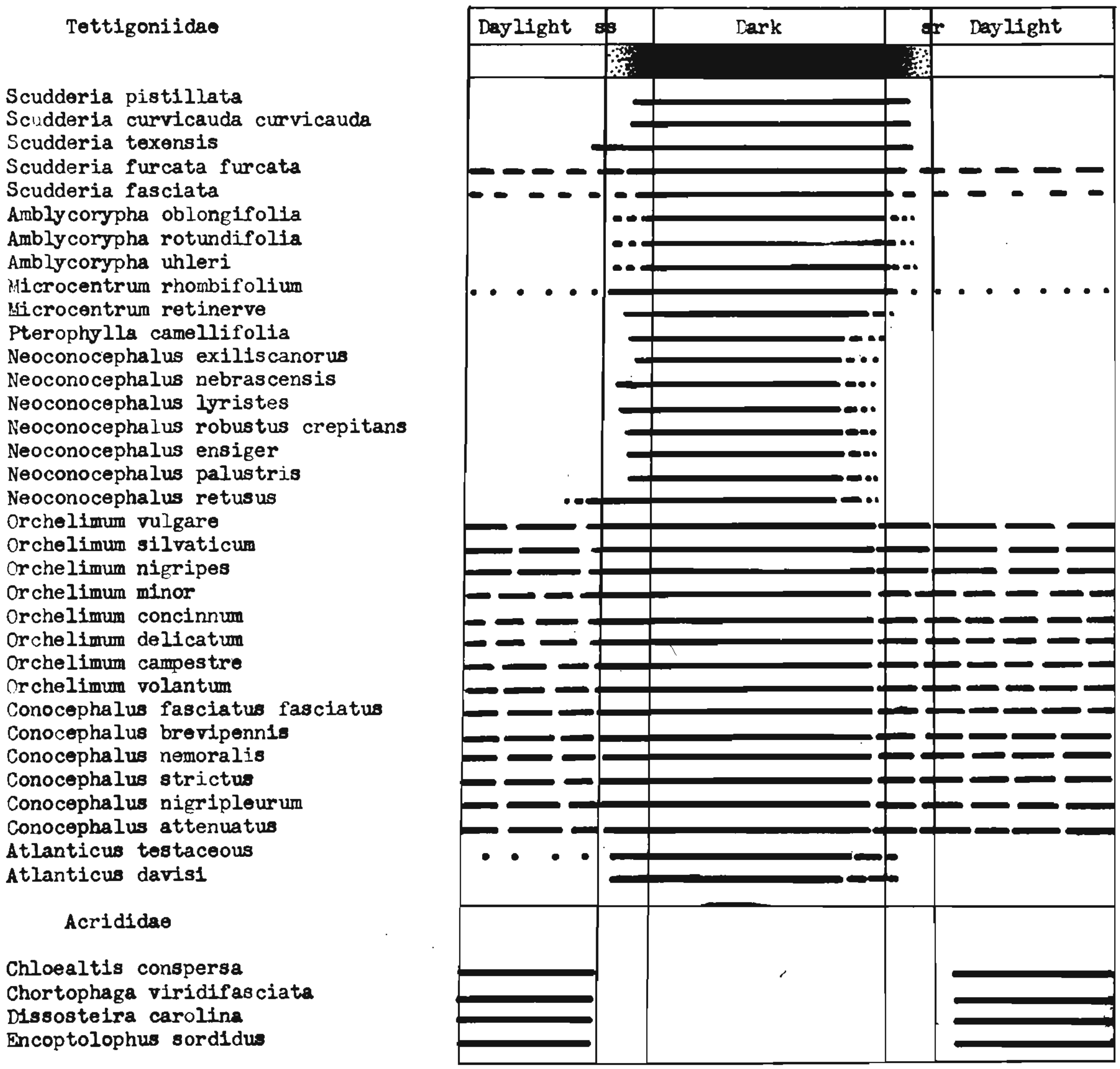


Fig. 38

Shortly after sunrise the loud songs of the cicadas take over the dominating role held by the night-singing Orthoptera from dusk till after midnight.

Ecologically, the various species of Orthoptera and Cicadidae can be found singing from the tops of the tallest trees to below the surface of the ground. The ecological distribution of singing insects in several different kinds of areas that occur in Ohio are shown in Plates XX-XXII. In general, those species that sing from perches on plants of various sorts can be classified according to the height at which they can be found. Thus, Pterophylla is scarcely ever found below ten or fifteen feet from the ground unless there is no vegetation taller than this in the area. Oecanthus niveus is generally a bush inhabitant found from 4-8 feet off the ground, and rarely above or below these limits. Most of the Orchelimum will be found from 4-6 feet above the ground, while the Conocephalus are rarely found more than 2-3 feet above the soil. The Scudderia perch horizontally on the tallest herbaceous vegetation in the area, whereas the Neoconocephalus species are most often found perched vertically on plant stems down inside the herbaceous vegetation. If a trilling tree cricket is heard from a perch 3-4 feet or more above the ground on coarse weeds, it will almost invariably be one of three species, Oecanthus nigricornis, O. argentinus, or O. latipennis. If the perch is within two feet of the ground, on grasses or fine-stemmed plants, the insect is almost certainly O. quadripunctatus.

PLATE XX.

ECOLOGICAL DISTRIBUTION OF SINGING INSECTS IN THE OHIO STATE UNIVERSITY WOODLOT

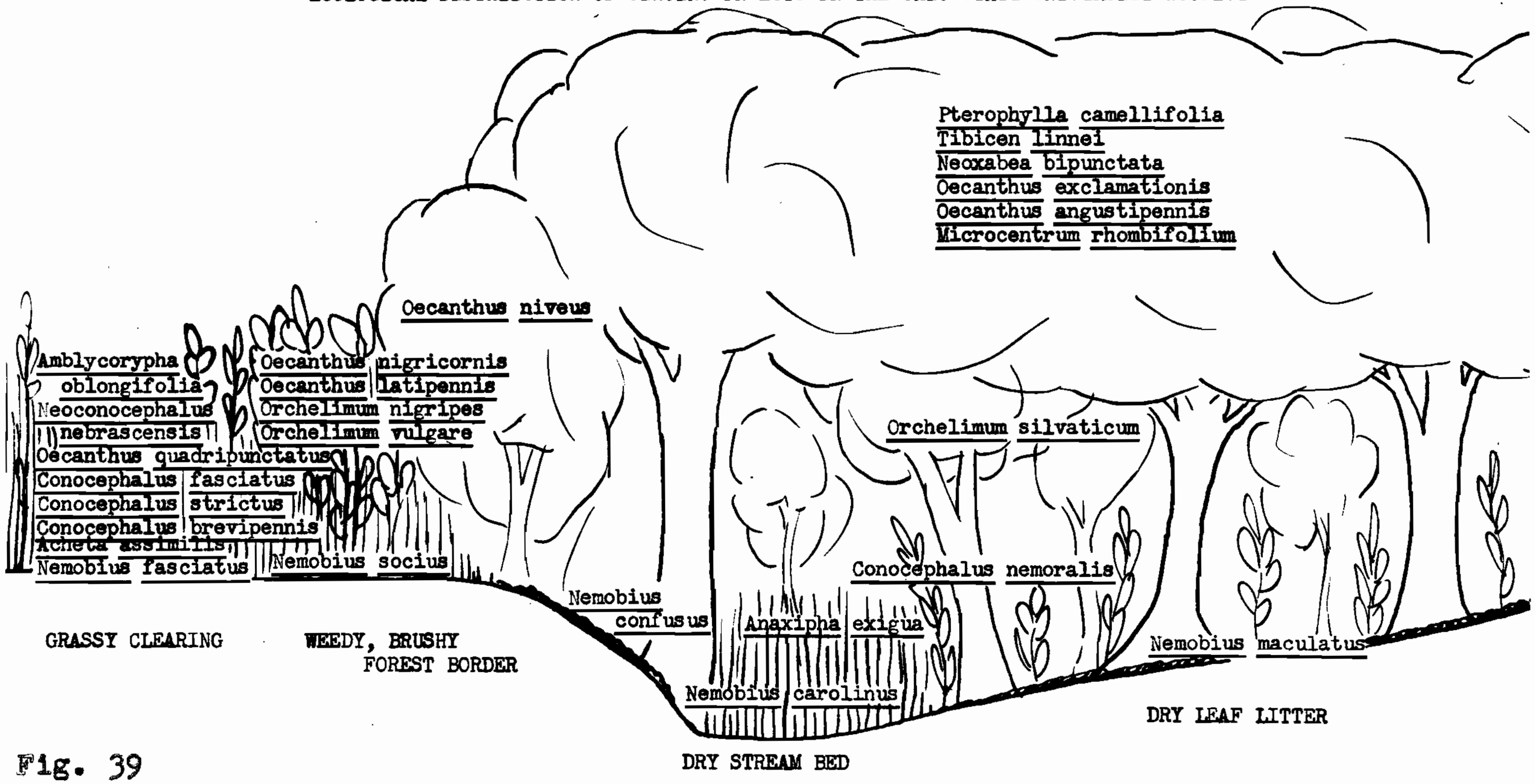


Fig. 39

PLATE XXI.

ECOLOGICAL DISTRIBUTION OF SINGING INSECTS IN A PICKAWAY COUNTY, OHIO, SWAMP FOREST

AND ALONG A MARSHY STREAM

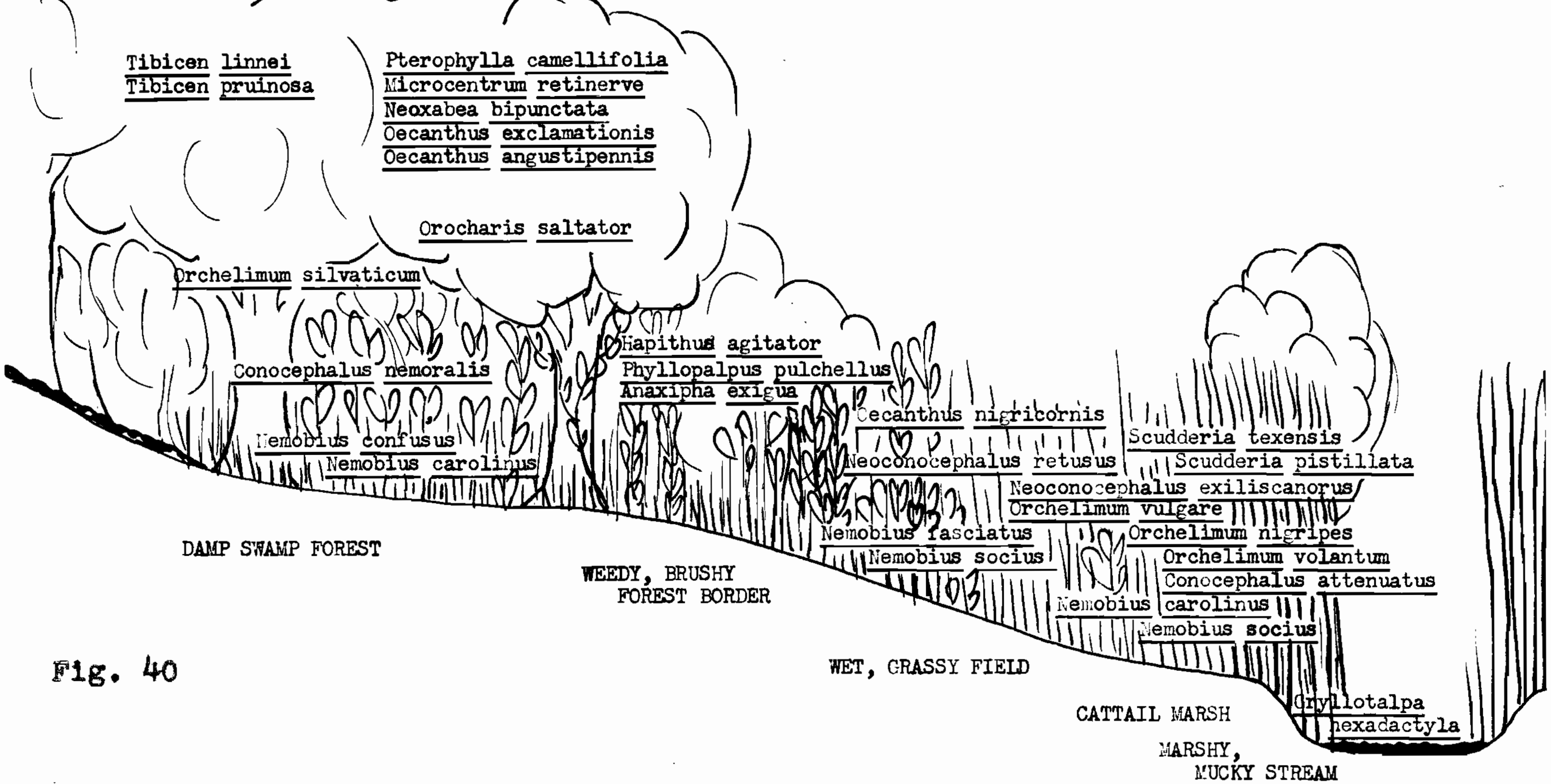


Fig. 40

PLATE XXII.

ECOLOGICAL DISTRIBUTION OF SINGING INSECTS ON A HILLSIDE IN HOCKING COUNTY, OHIO

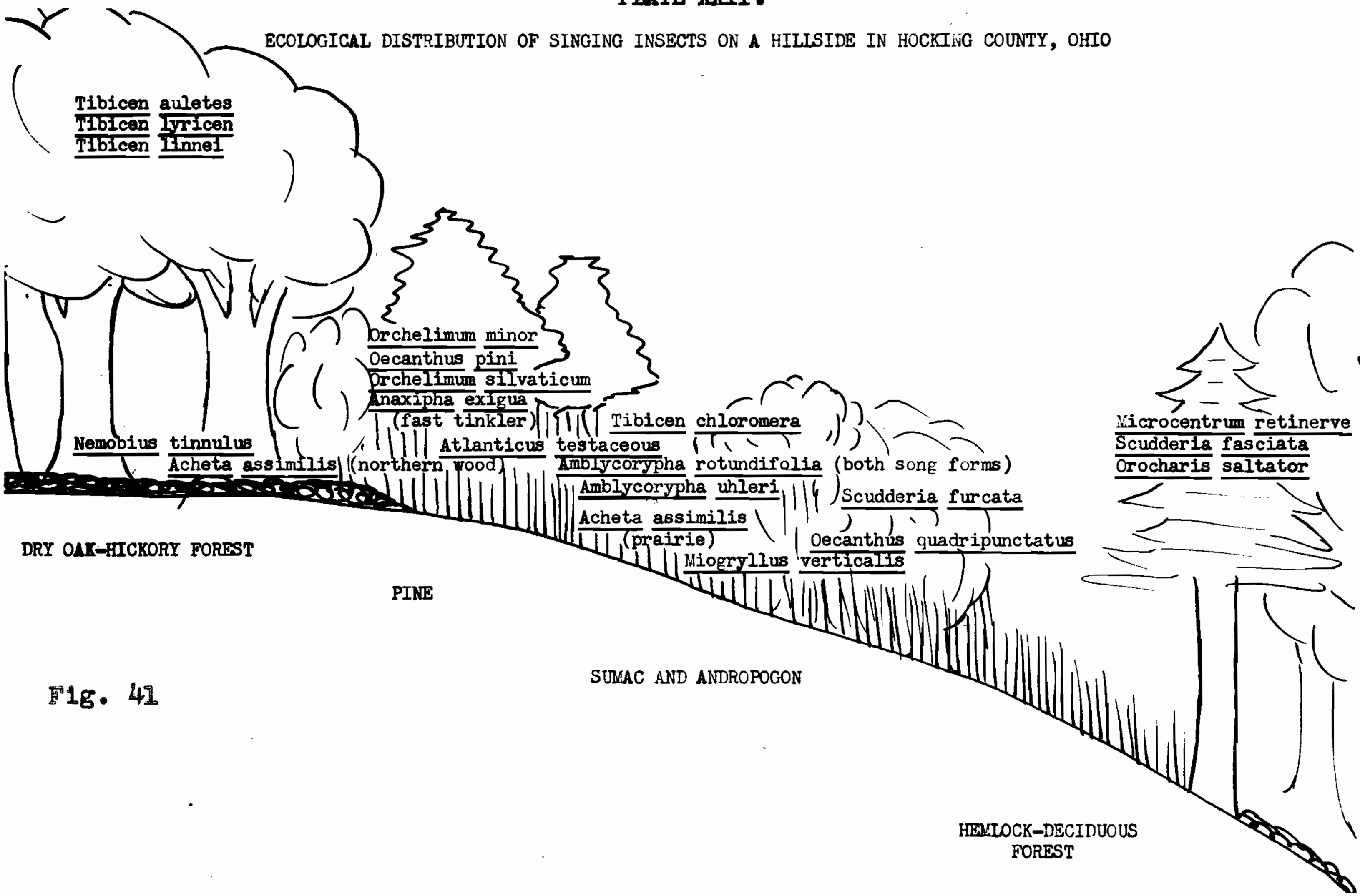


Fig. 41

Different species vary in their "wariness," or as to how easily they can be approached while singing without being disturbed. *Orchelimum glaberrimum* often stops singing when approached at a distance of several yards; *Conocephalus nemoralis* will sometimes continue to sing while dodging one's hand. Some species, such as the *Scudderia*, fly when disturbed; *Pterophylla* often glides to the ground or to a lower perch; the *Neoconocephalus* drop quickly to the ground and "freeze," often with their head buried in the grass; *Conocephalus attenuatus* jumps repeatedly, usually until it has travelled several yards from the spot at which it was originally disturbed.

Gryllidae, Gryllinae

The Ground Crickets

The ground crickets, as their name implies, are found on the ground in a variety of habitats. Various species can be heard singing from early May until after the first heavy frosts at Columbus, Ohio. Most species have but one generation per season and overwinter in the egg stage, but a few species of *Acheta* overwinter as late instar nymphs, and at least one species has two generations per season (triller *Acheta*, North Carolina).

All the ground crickets sing both day and night, but many species do most of their singing at night. Most species have well-defined courtship songs, and fight chirps. The tegmina are lifted to about a 45° angle with the body during the calling song, and flattened and tilted roof-like over the abdomen during the courtship song. The female mounts the male, over the flattened tegmina, during copulation. There are no female-attracting metanotal glands, but in some species of *Nemobius* the males have glands on the hind tibiae which apparently have a similar function.

Male Gryllinae exhibit varying degrees of sedentariness. Their songs are clear chirps or trills of varying complexity, the pitch ranging from 4 to 9 kilocycles per second, depending on the size of the singer. No synchronization or alternation is known in these, or any other ground-inhabiting species.

Native American *Acheta*
The Field Crickets

Native field crickets in the genus *Acheta* occur all over North, South, and Central America, in the West Indies, the Galapagos, and on many other islands. Within this area they can be found almost everywhere except at very high altitudes and in extremely moist or arid situations. They are large, commonplace, easily captured insects with many prominent morphological features. Yet no satisfactory systematic analysis of even a small part of the genus has been produced. The first description of an American field cricket was published in 1775 (Fabricius, 26), and an almost uninterrupted flow of taxonomic papers dealing with the group has continued since. Forty-seven names had been applied to American field crickets by 1903. Lutz in 1908, 26, and Rehn and Hebard in 1915, 26, after studying large series of specimens, concluded that only one highly variable species was represented. Since 1915 all the native field crickets have been lumped together under the name Acheta assimilis Fabricius, the type of which is from Jamaica.

Practically all the early workers on this group considered morphology alone; such characters as size, coloration, wing venation, body proportions, number and relative lengths of tibial spines, and the length of such parts as tegmina, wings, ovipositor, and hind femora were most often discussed. A wide range of variation exists in most of these characters. American field crickets range from 12.8 mm. to 28.8 mm. in body length, and from solid black to pale straw in color. In general, forms that are morphologically similar in different localities can be found in three types of habitats: (1) large, light-colored forms in sandy areas (beaches, sand dunes, deserts, etc.), (2) small, black forms in deciduous forests, and (3) forms intermediate between these two extremes in grassy and weedy areas such as prairies, fields, pastures, roadsides, and lawns. Rehn and Hebard (1915, 26) recognized this ecological distribution of morphologically similar forms, but because no discontinuities existed with respect to the characters they observed, described them as "...mere variations, the adaptions of this exceedingly plastic species to local environmental conditions." They further stated "...none of these are distinct either specifically or as geographic races, and really show only the various phases resultant from varied environmental conditions."

Blatchley (1903, 6) was the only investigator to supply detailed biological information along with description of new species. A number of workers, such as McNeill (1889, 26) in Illinois, Allard (1910b, 6) in Georgia and New England, Severin (1935, 26) in North Dakota, Ball (1942, 26) in Arizona, and Cantrall (1943, 6) in Michigan, noted variations in life history and song in the field crickets they observed in these different parts of the country. In 1952, B. B. Fulton published a study of the field crickets of North Carolina in which he described four populations that differed in ecology, life history, song, and distribution, but had no distinguishing morphological features. These four populations failed to interbreed in fifty attempts. In 1953, Dr. Edward S. Thomas of the Ohio State Museum told this writer that he had known for some time that at least two different kinds of field crickets occurred in Ohio, with differences in ecology and song. The present study, conducted over the past three years in Ohio, Indiana, and Illinois, has revealed at least three species of field crickets in this area which not only differ in ecology, life history, and song, but are also morphologically distinguishable in at least one sex. Comparison of these species with Fulton's field crickets shows that at least one, and possibly two are different from his, making a total of five or six species of field crickets now known in eastern United States. The complexity of the situation makes it not surprising that conventional taxonomic techniques have failed in its analysis. It is hoped that the results presented here will stimulate further study of this interesting genus in the great part of its range that is yet unexplored.

Nomenclature

It is this writer's opinion that the species discussed here should eventually receive formal scientific names. However, there are forty-six names available for American Acheta from descriptions based primarily or entirely on morphology. Since some of the presently defined species can be distinguished morphologically, at least in one sex, and in others there are recognizable extremes in some morphological characters, it is believed that formal names should not be attached to any of them until the types of the species defined by earlier authors have been examined. Consequently colloquial or "common" names will be used in the present discussion. The three species which occur in Ohio will be called the mountain cricket (same as Fulton's mountain cricket), the northern wood cricket, and the prairie cricket. Fulton's crickets will be referred to as the beach cricket, the southern wood cricket, the triller cricket, and the mountain cricket. The prairie cricket and the southern wood cricket may be parts of a single species, but because they occur in somewhat different habitats (in North Carolina and Ohio), and because of crossing experiments and other observations carried out by this writer, using only the prairie cricket, or northern form, they will be considered separately in the present discussion.

Distributional Relationships

The known distribution of the eastern field crickets, based almost entirely on the collections of Fulton and the present writer, is shown in Plate XXIII. More investigation is needed to determine the southern limits of the northern wood cricket and the prairie cricket, and the northern limits of the southern wood cricket. The western limits are not known for any of the northern populations, nor are the eastern limits. The northern wood cricket is known only as far north as Vermillion County, Illinois, and Delaware County, Ohio, but probably extends farther north. It is probable that it is the mountain cricket which extends up into Canada to the northern limits of *Acheta* in eastern North America. The mountain cricket is apparently the same as Cantrall's field cricket on the George Reserve, Michigan, and specimens collected and recorded (song) by D. J. Borror near Medomak, Maine, appear to be mountain crickets.

The prairie cricket is limited on the north, in Ohio, Indiana, and Illinois, to within a few miles of the glacial boundary. Its northern limits have been traced very carefully in Hocking and Fairfield Counties in Ohio.

The mountain cricket extends southward below the Appalachian mountains where its range overlaps broadly with that of the southern wood cricket and the triller.

Ecological Relationships

The mountain cricket occurs in almost all kinds of grassy

PLATE XXIII. GEOGRAPHIC DISTRIBUTION OF EASTERN FIELD CRICKETS

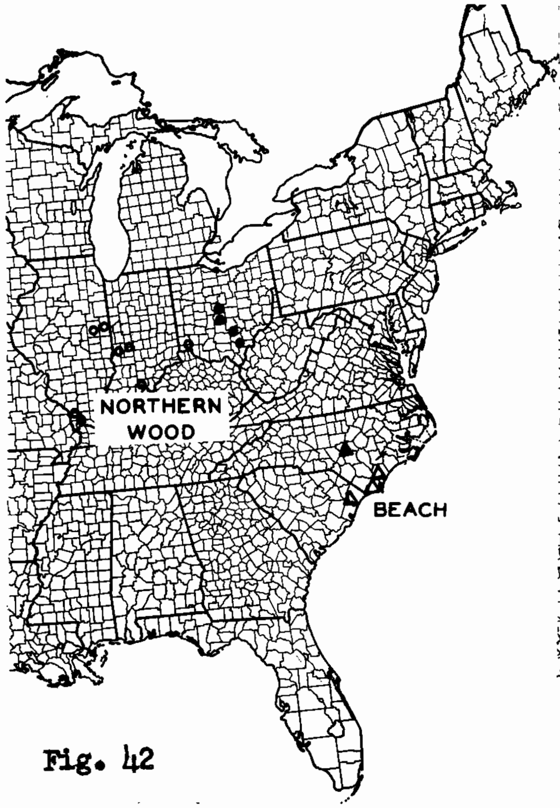


Fig. 42

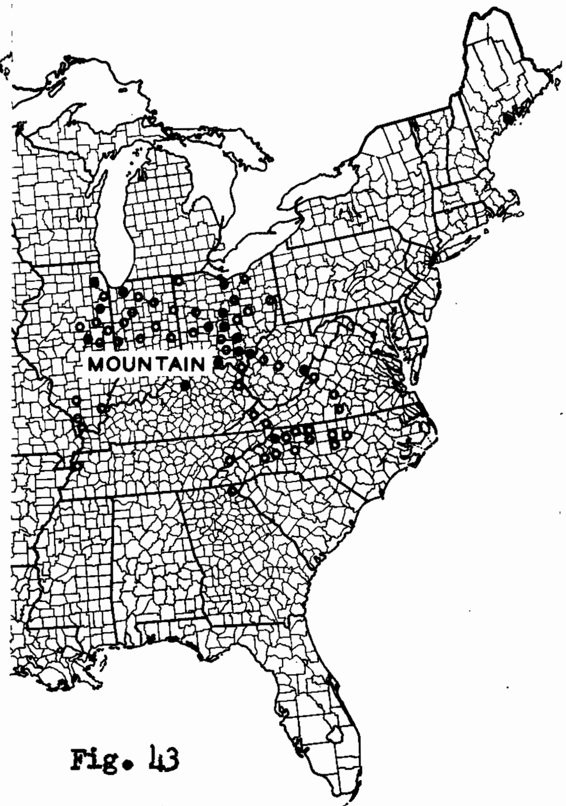


Fig. 43

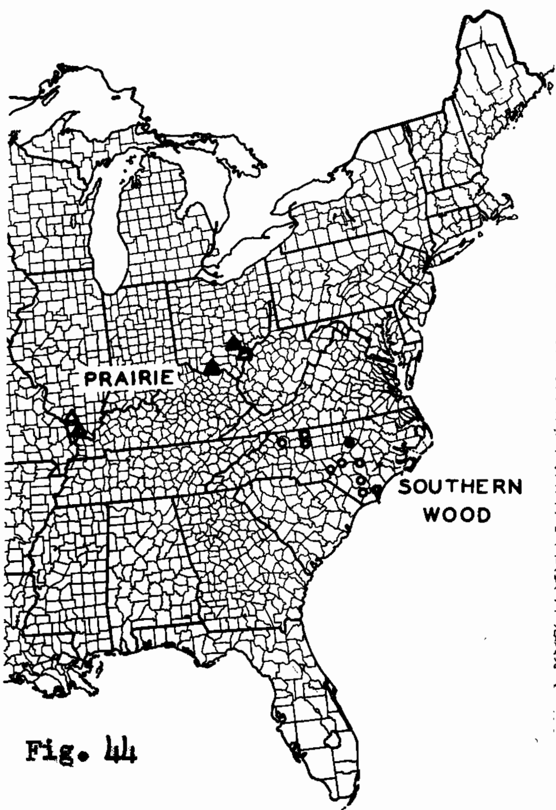


Fig. 44

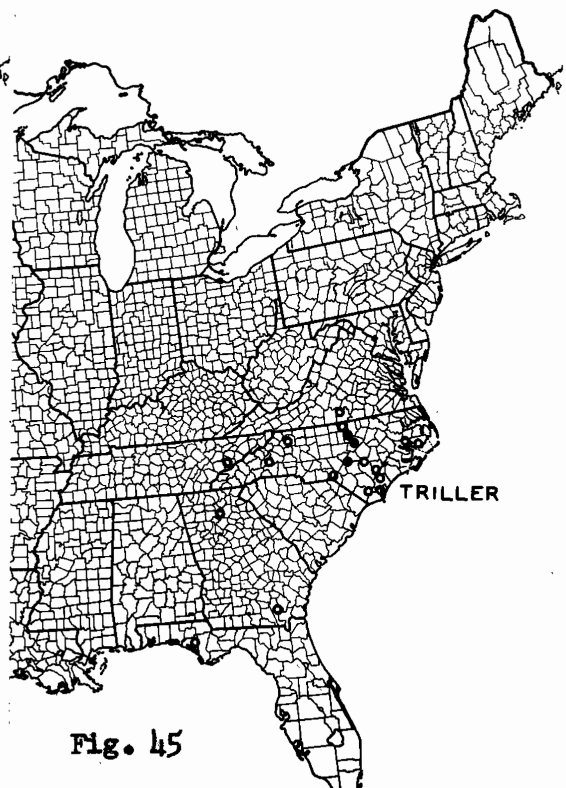


Fig. 45

situations, such as fields, pastures, weedy areas, roadsides, and lawns, and it represents a large proportion of the field cricket population in Ohio, Illinois, and Indiana. It is much easier to collect than either of the other two northeastern crickets, and therefore dominates collections of Acheta in this area. Prairie and northern wood crickets sing very little in the daytime, and are difficult to locate and capture in the Andropogon clumps and leaf litter in which they occur, respectively.

Table 2

Relative Numbers of Mountain, Prairie, and Northern Wood Crickets in Several Collections in Ohio, Indiana, and Illinois

Location of Collection	Numbers of Acheta Specimens			
	Mountain	Northern Wood	Prairie	Total
Ohio State Museum	266	51	2	317
Ohio State University	81	2	none	83
Purdue (Blatchley)	38	5	3	46
Illinois Natural History Survey	229	8	none	237
Totals	614	69	5	685

The northern wood cricket is found in leaf litter in deciduous forests. In some areas gradual transition from continuous leaf litter through patchy leaf litter to open pasture causes a wide zone of overlap with the mountain cricket. One such area in Franklin County, Ohio, was studied rather painstakingly. An overlap zone of

PLATE XXIV.

ECOLOGICAL DISTRIBUTION OF FIELD CRICKETS IN SOUTHERN OHIO

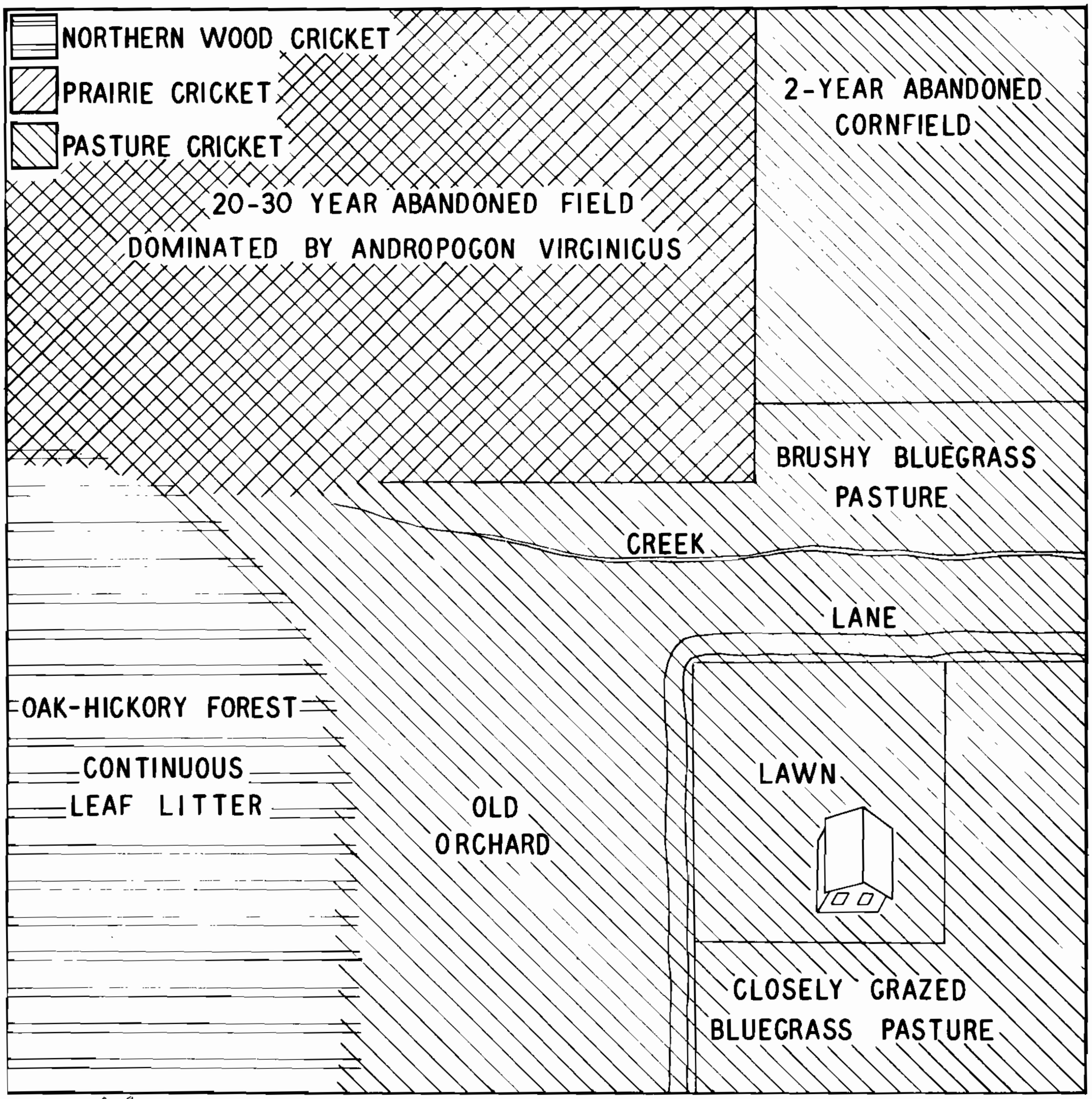


Fig. 46

from 30 to 40 feet wide existed, with patches of leaf litter 3 or 4 feet in diameter occurring about the same distance apart within it. Mountain crickets are generally found near burrows of their own making or under stones, boards, trash, or dried cow dung. A number of them were collected from such places within this overlap zone, and one was heard singing in a patch of leaf litter. No wood crickets were found under stones or cow dung, although specimens were seen in nearly every patch of leaf litter in the area. In another locality studied, a fence line separating a pastured woodlot from an unpastured one caused an abrupt transition from continuous leaf litter to open bluegrass pasture with practically no leaf litter. A colony of wood crickets extended up to the fence on the unpastured side and was so dense that over a hundred adults were collected by hand in less than an hour. On the pastured side of the fence, mountain crickets were singing and no wood crickets could be found. One mountain cricket nymph was collected about ten feet inside the woods.

The prairie cricket occurs on dry hillsides dominated by *Andropogon virginicus* or *A. scoparius*. In southern Ohio it is found in old fields, 20-30 years abandoned, which are dominated by *A. virginicus*. As shown in Plate XXIV, the mountain cricket also occurs in these fields, and the two seem to be randomly mixed in such areas. In southwestern Ohio and along the Mississippi River bluffs, the prairie cricket occurs in the hilltop prairie openings dominated by *A. scoparius*. In several such areas in southern Illinois the prairie cricket was the only field cricket heard or collected. One adult male of the northern wood cricket was collected in the woods along the border of one of these prairies, and pasture crickets were collected and heard singing in some of them, as well as in fields and along roadsides. The prairie cricket is often found in greatest numbers along the forest borders around the characteristic *Andropogon*-covered hillsides over which it spreads. In southern Ohio, all three of these crickets sometimes occur together in narrow zones of overlap.

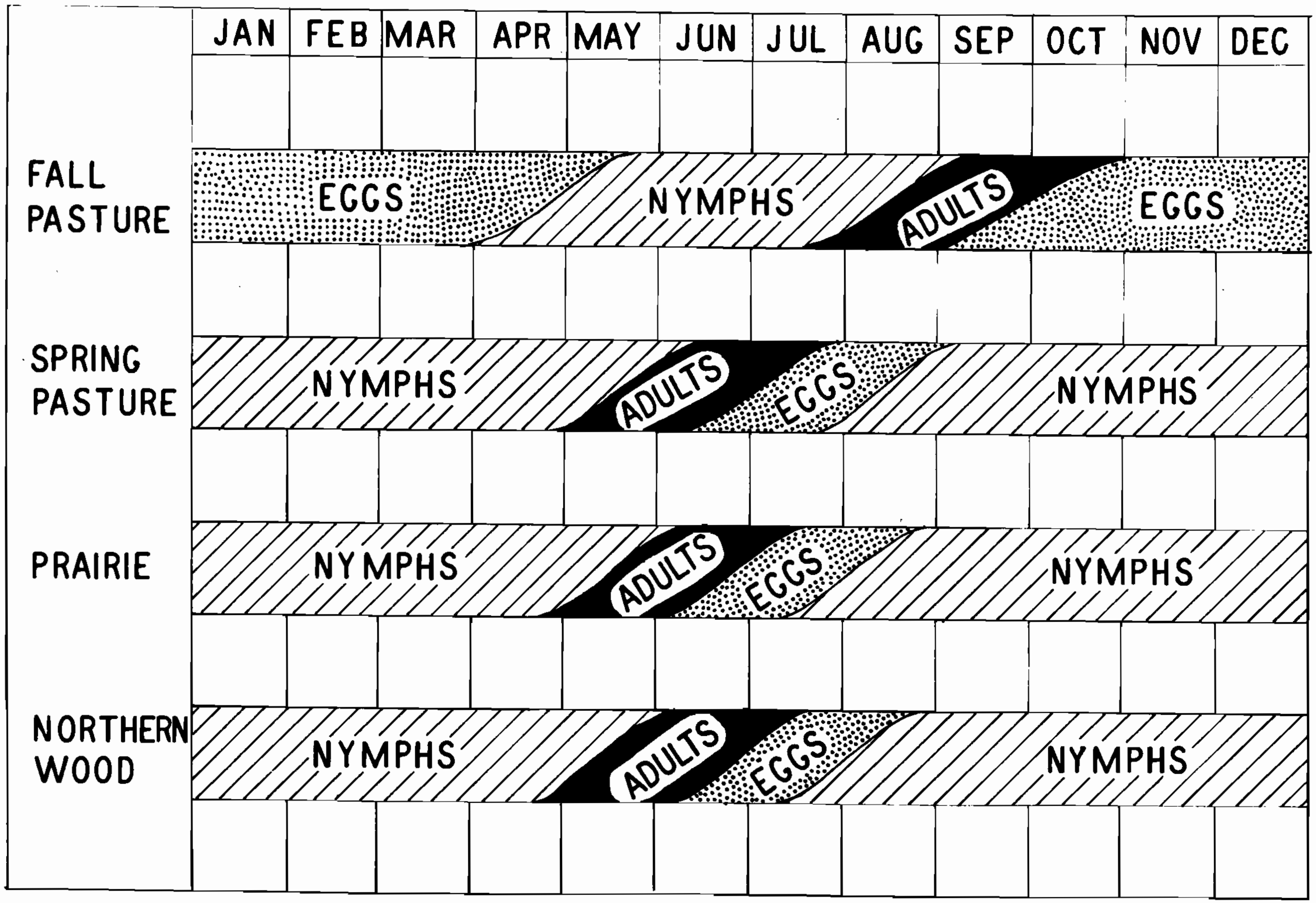
Seasonal Life Histories

The seasonal relationships of the Ohio field crickets are shown in Plate XXV. The northern wood cricket and the prairie cricket produce adults in spring while the mountain cricket consists of two populations, one of which produces adults in spring, and another which produces adults in late summer and fall. Fulton's southern wood cricket is a spring cricket, his beach cricket is a fall cricket, and his triller produces two generations per season. The series of 1504 specimens studied by Rehn and Hebard contained less than 100 spring crickets from eastern United States. This is rather important in view of the fact that two out of the three morphologically distinct Ohio species are spring crickets, and the other has both a spring and a fall population.

No way of distinguishing the spring and fall mountain crickets has been found other than the differences in their seasonal life

PLATE XXV. Fig. 47

SEASONAL LIFE HISTORIES OF OHIO FIELD CRICKETS



histories. One population overwinters as partly grown nymphs and produces adults which sing from early May till mid-July. The other overwinters in the egg stage and produces adults which sing from mid-July till frost. These two populations apparently occupy the same habitat, and songwise and structurally they are practically identical. There is a slight overlap of adults in mid-July. Although very few adults can be seen or heard in mid-July, no night occurred from May to October during the two years of this study when mountain crickets were not singing on the Ohio State University Campus. Nine attempts to cross spring and fall adults in the laboratory have failed, but a high percentage of failures among controls run at the same time makes the results of this test doubtful.

The indications are that offspring of the spring population of the mountain cricket never mature in fall. No adults or last instar nymphs have ever been taken overwintering. Last instar nymphs of the fall population can be found on the Ohio State University Campus up to mid-September, but later in the fall only adults and young nymphs of the spring population, about three instars from adulthood, can be found. In the laboratory, the offspring of Franklin County, Ohio, spring adults mated on May 4 started maturing as early as August 12. However, a few individuals in these same cages had not yet reached the last nymphal instar by mid-October. Another pair of spring adults from Piatt County, Illinois, was mated on June 6 and removed from the cage on July 11. Their offspring began maturing in October, but the last did not mature until the following April.

Similar results have been obtained by Dr. Phillip Stone with the offspring of a single field cricket picked up near Columbia, Missouri (Personal communication). Dr. Stone said that while about 95% of these offspring matured in around 90 days, the other 5% required nearly a year.

Neither the prairie nor the northern wood cricket mature in the fall in the field, and both produced offspring from early May matings in the laboratory which began maturing in mid-August and early September, respectively. This discrepancy may be due to the high-protein dog food diet used in laboratory cultures, to higher temperatures, or to some other factor or combination of factors.

Fulton's findings in North Carolina indicated that offspring of spring adults may sometimes mature in the fall, while Cantrall failed to obtain any fall adults from seven pairs of spring population adults caged outside on June 9 in Michigan. In North Carolina the spring population is much larger than the fall population, while on the George Reserve, Michigan, only about 5% of the total are spring crickets, due, Cantrall believes, to high mortality among over-wintering nymphs. In central Ohio, no noticeable difference in numbers occurs between the spring and fall populations. These two populations may interbreed in mid-summer, or in the southern part of their range possibly in fall, or it may be that they have been isolated such a short time that no noticeable differences have yet appeared between them. Certainly more investigation is needed to clarify their relationship.

The northern wood cricket and the prairie cricket overwinter as partly grown nymphs, and during the two seasons that this study has been in progress, they apparently began to mature a week or two earlier than the spring mountain cricket in southern Ohio, beginning to sing in late April or early May. No adults of these two populations have ever been collected or heard in the field after mid-July. Fulton indicates that his southern wood cricket begins to sing in mid-April and continues until early August. He says that in a cage of adults the last male died on August 1, but some females lived until sometime between August 20 and August 26. This writer collected an adult male and heard several singing on August 10, 1955, near Raleigh, North Carolina. One of the males collected was mated with a prairie cricket female from Hocking County, Ohio, on August 18, and was still alive on September 19. Offspring from this mating appeared on September 30.

Song Relationships

Geographic variation in the songs of field crickets was first noted by Allard (1910b, 6); Fulton (1952, 6) first used it as a taxonomic character in this group. The species discussed here were discovered first of all, and perhaps only because of differences in their songs.

The different sounds produced by a male field cricket in several different situations are shown in Plate XXVIII. Due to the fact that cultures of field crickets have been kept in the laboratory almost

PLATE XXVI. SOLITARY SONGS OF ACHETA

FREQUENCY IN KILOCYCLES PER SECOND

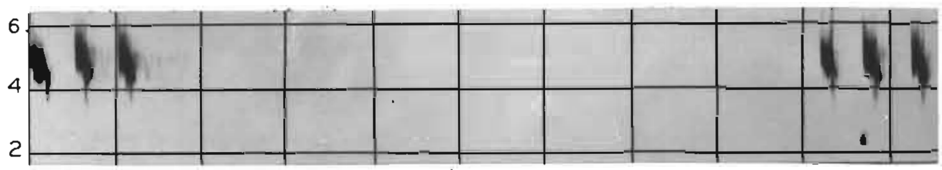


Fig. 48. HOUSE CRICKET

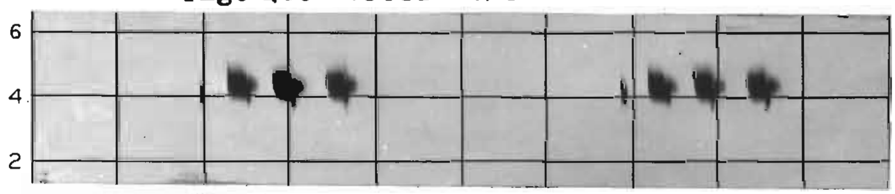


Fig. 49. BEACH CRICKET

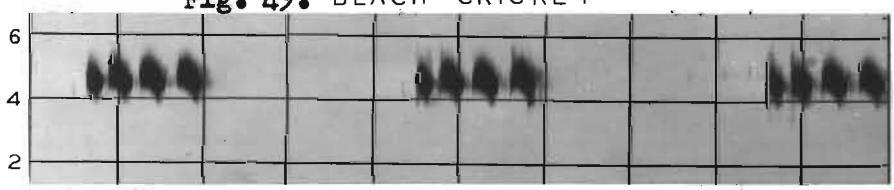


Fig. 50. PASTURE OR MOUNTAIN CRICKET

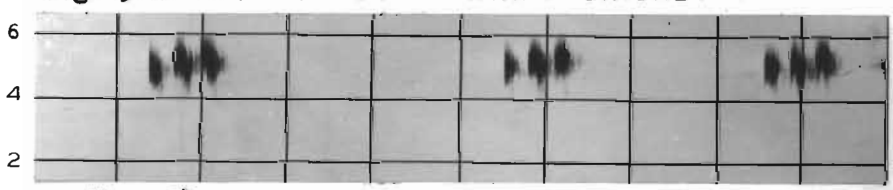


Fig. 51. NORTHERN WOOD CRICKET

Fig. 52. PRAIRIE CRICKET

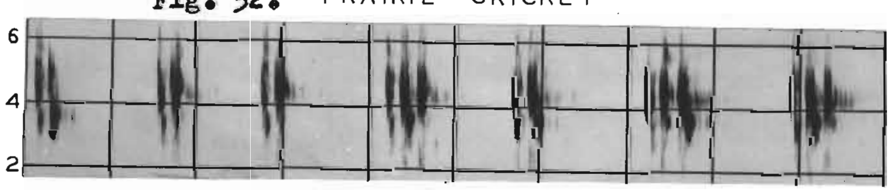


Fig. 53. SOUTHERN WOOD CRICKET

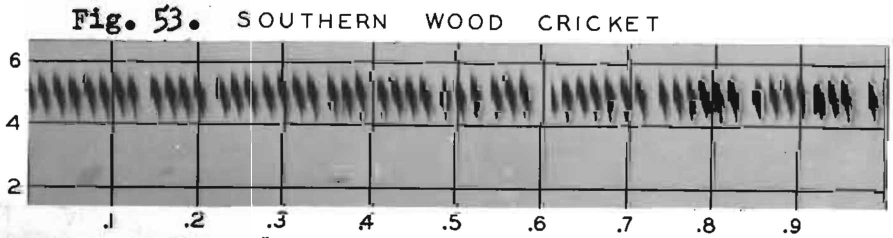


Fig. 54. TRILLER CRICKET

TIME IN SECONDS

PLATE XXVII. PULSE RATE VERSUS TEMPERATURE IN THE CALLING SONGS OF EASTERN FIELD CRICKETS

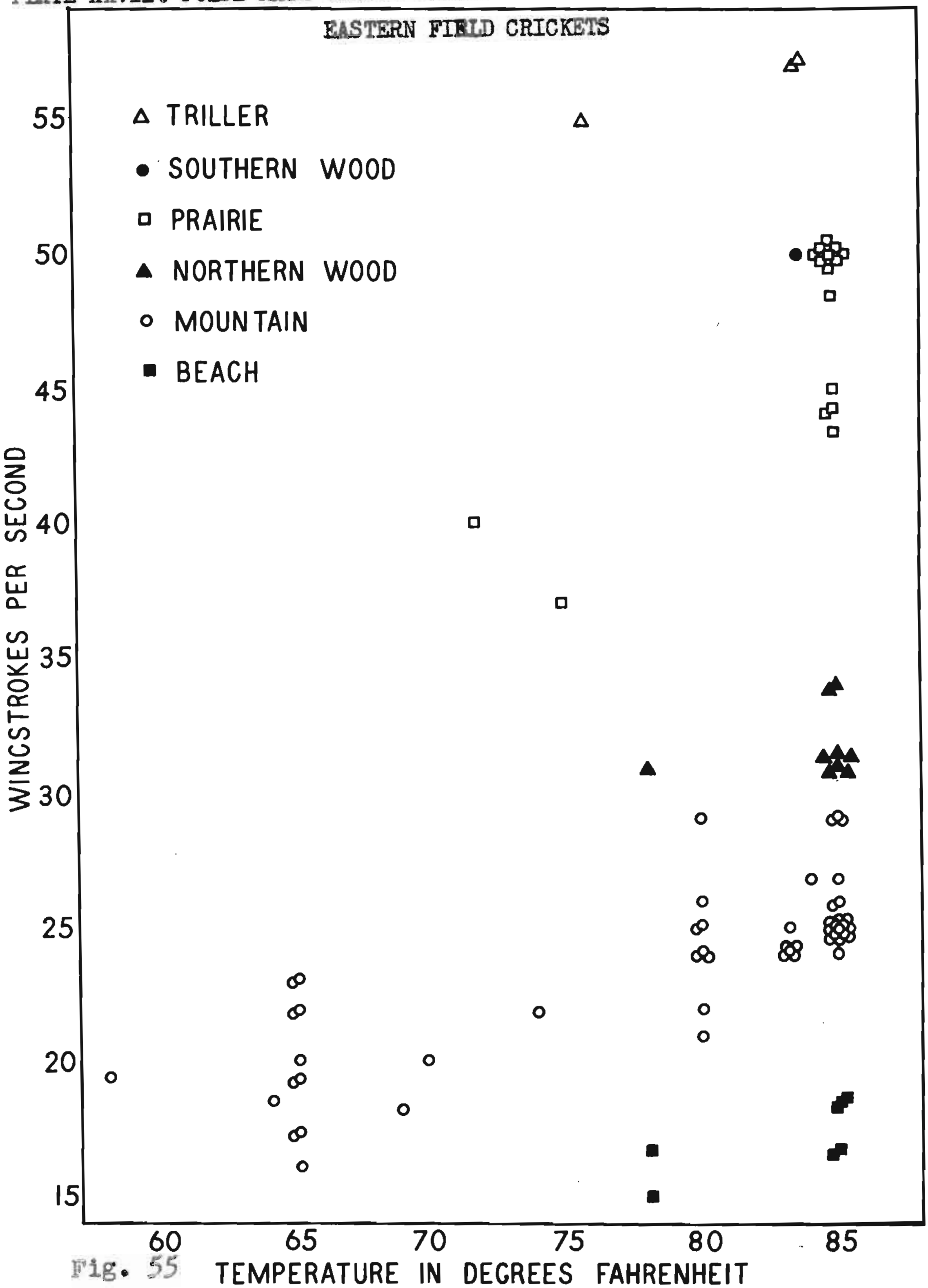


Fig. 55

PLATE XXVIII.

VARIATIONS IN FIELD CRICKET SOUNDS WITH CHANGES IN SITUATION (MOUNTAIN ACHETA)

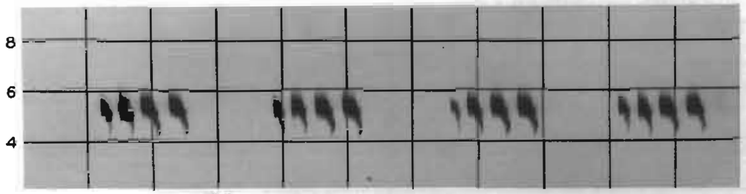


Fig. 56. CALLING SONG

Fig. 60. MIXED COURTSHIP

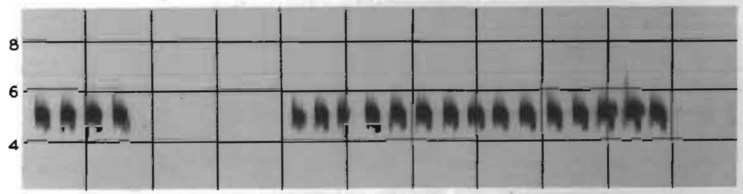


Fig. 57. APPROACH OF MALE

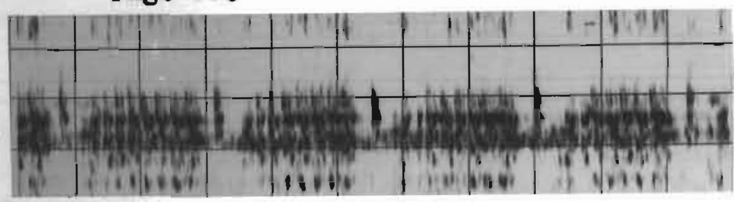


Fig. 61. FULL COURTSHIP SONG

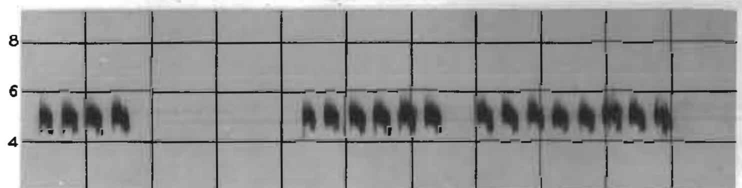


Fig. 58. APPROACH OF FEMALE

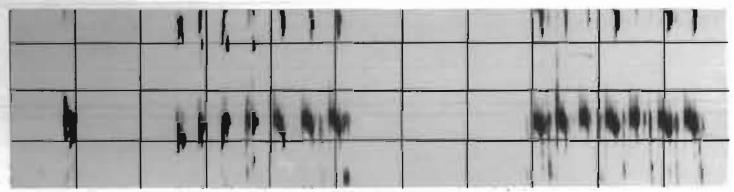


Fig. 62. INTERRUPTION OF COURTSHIP

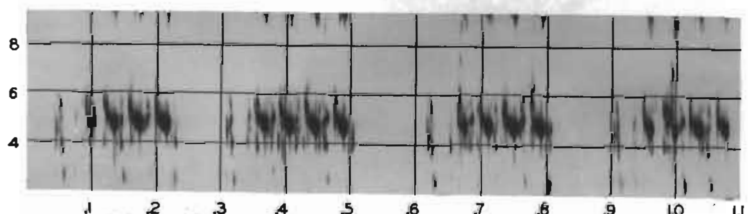


Fig. 59. PRE-COURTSHIP
TIME IN SECONDS

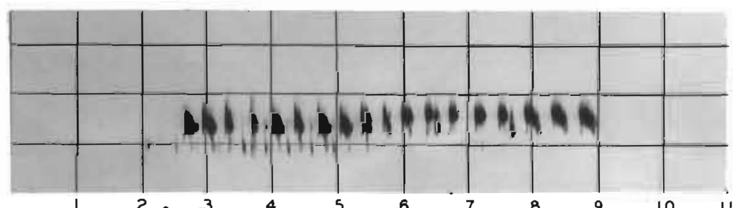


Fig. 63. DEPARTURE OF FEMALE
TIME IN SECONDS

continuously for the past two years, and one large aquarium with several specimens in it on my desk most of the time, the situations evoking the several different sounds of this species have been observed over and over again. Parallel modifications occur in the sounds of the other field cricket species and the house cricket, Acheta domesticus L. With any of these species, one eventually reaches the point of being able to tell exactly what is going on in a culture without looking, due to the types of sounds being produced.

As with most singing Tettigoniidae and Gryllidae, adult male field crickets tend to space themselves in the field and to remain in one spot all their lives. A large part of the time they produce the calling or solitary song. This song attracts the females which move toward and locate the males. Females are seen much more often in the field and dominate collections of Acheta for this reason.

When a singing male is approached by another male, he stops the regular chirping of the calling song and delivers one or more louder, clearer, and longer chirps (containing more wingstrokes). The two individuals may stand an inch or so apart, facing each other, and chirp in this manner for several seconds, or they may move together and engage the mandibles and scuffle, sometimes turning and kicking each other with the hind femora. Eventually one of the males leaves, sometimes after only exchanging chirps, sometimes after physical contact. The remaining male will then usually take up the calling song again.

When a male singing the calling song is approached by a female, or often when a male walking around a cage encounters a female, he will usually produce a few chirps very similar to those produced when another male is encountered — loud, clear chirps containing a large number of pulses. The chief distinction between this type of chirping and that produced in an encounter between males is that it grades rather continuously into what has been arbitrarily designated as "pre-countship singing," and if uninterrupted, eventually into "mixed countship singing," and the full courtship rhythm. "Pre-courtship" singing is made up of sequences of one- or two-pulse chirps, somewhat softer and less musical than those produced in the calling song and delivered at rather even rates of 2-3 per second. Mixed courtship singing is the type of courtship song most commonly heard in a culture. It apparently represents a stage between pre-courtship and full courtship which is maintained for long periods of time, presumably when the female is not fully stimulated by the courtship activities of the male, either because of her physiological condition, or because of some weakness in the courtship sequence. As long as the female remains in the vicinity of a courting male, but does not allow him to back under her or come into physical contact, the mixed courtship singing is the type produced. It consists of a mixture of soft pulses characteristic of courtship with the loud, musical pulses characteristic of the calling song, fight song, female encounter, and courtship interruption.

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

During courtship singing, in addition to backing toward the head end of the female, the male sways from side to side, and flattens his body against the substrate, especially as he comes into contact with the female. If the female is responsive, she either mounts on top of the flattened tegmina, or simply allows the male to back under her, and the spermatophore is transferred in this position. It is presumed that the courtship song may either be necessary for the accomplishment of successful copulation, or it may at least shorten the time between meeting of the sexes and copulation. It is noteworthy that most of the crickets which do not possess courtship songs generally have dorsal female-attracting glands, which certainly "draw" the female into the copulatory position.

Tape recordings and Vibragrams have been made of the calling or solitary songs of 103 field crickets from Ohio, Indiana, Illinois, Virginia, West Virginia, Tennessee, Kentucky, North Carolina, and Maine. Plate XXVI shows Vibragrams of the solitary songs of the six field cricket populations under consideration, and of the house cricket, Acheta domesticus L., a species introduced from Europe. A number of analyzable characteristics appear in Acheta sounds, such as the frequency in cycles per second, rate of toothstrike (individual toothstrikes are not shown in Plate XXVI), rate of pulsation (or wingstroke rate), rate of chirping, regularity of chirping, and number of pulses per chirp. Plate XXVII is a scatter diagram comparing the songs of all individuals recorded with respect to one character, rate of wingstroke, or pulsation. This is plotted against temperature.

All of the eastern field crickets sing both day and night, though the northern wood cricket, the southern wood cricket, and the prairie cricket do the vast majority of their singing at night. The songs of these three crickets are soft and somewhat creaky when compared to the loud, clear chirps of the mountain cricket and the beach cricket. They chirp more rapidly and more regularly than do the mountain cricket and the beach cricket, with the northern wood cricket being somewhat intermediate in these respects. In some cases, there may be considerable variation in the chirping rate of a single individual. Male mountain crickets caged alone in the laboratory generally begin singing at rates of about 120-150 chirps per minute.

As these lone males grow older their chirp rate increases more or less steadily up to at least 300 chirps per minute. One virgin male timed three weeks after molting to adulthood was singing steadily at a rate of 370 chirps per minute.

Although in some cases other characters are most distinct and more easily used, song differences have proven better than any other single set of related characters for separating all of the Acheta species distinguished so far. Due primarily to the fact that several characteristics can be compared, the recorded songs of all species can be separated by spectrographic analysis with practically 100% accuracy. Not enough courtship songs have been recorded to make comparisons.

Morphological Characteristics

The morphological characters found to be of value in this study were body proportions, size, coloration, and length of the tegmina, wings, and ovipositor. A large number of other characters, including wing venation, structure of the male genitalia, and the number and relative lengths of the spines on the hind tibiae were examined, and none of value was discovered. No one character was found which would separate all six populations. No characters were found to separate the mountain, triller, and beach crickets from one another, nor the southern wood cricket from the prairie cricket. In most characters, the triller forms a partial bridge between two groups of morphologically similar populations (northern wood, prairie, and southern wood, and mountain and beach). However, it obviously cannot represent interbreeding or fusing of the two because of its distribution and its song. This is probably another reason why Lutz and Rehn and Hebard believed that no distinct entities existed in this genus. In attempting to deal with the whole genus at once, the distinctions between non-interbreeding groups were obscured by apparent intergrades which actually represented additional and quite different populations.

With respect to wing length, dimorphism is exhibited by the mountain, beach, and triller crickets, while only short-winged individuals have been collected in the field of the northern wood, southern wood, and prairie crickets. Some prairie crickets reared on a high-protein dog food diet, and under crowded conditions developed long underwings, but similar conditions have never produced long-winged northern wood crickets. Almost 100% of the mountain crickets reared under these conditions develop long wings. Earlier authors have considered this character to be of no value since it was discovered that short-winged parents may produce long-winged offspring and vice versa. Nevertheless, if the ability to develop long wings is completely lost from a population, a genetic change is indicated.

As shown in Plate XXIX, all species except the mountain cricket have the head invariably narrower than the pronotum. In these species, the pronotum is generally widest near its posterior margin. In the mountain crickets, especially the males, the reverse is true, with

PLATE XXIX. Fig. 64

RATIO OF HEAD WIDTH TO PRONOTAL WIDTH IN EASTERN FIELD CRICKET MALES

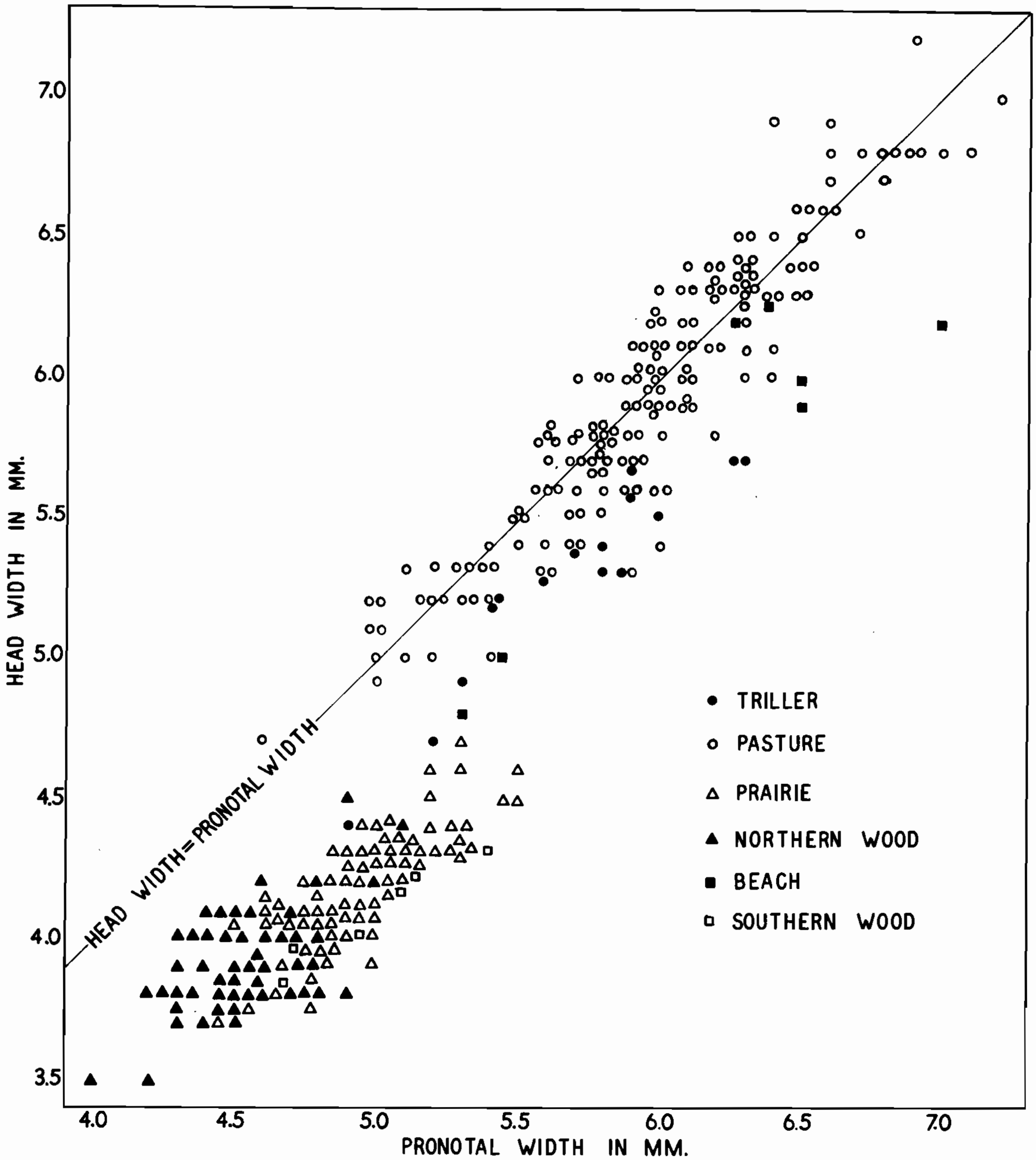


PLATE XXX. RATIO OF BODY LENGTH TO TEGMINAL LENGTH IN PRAIRIE CRICKET MALES AND NORTHERN WOOD CRICKET MALES

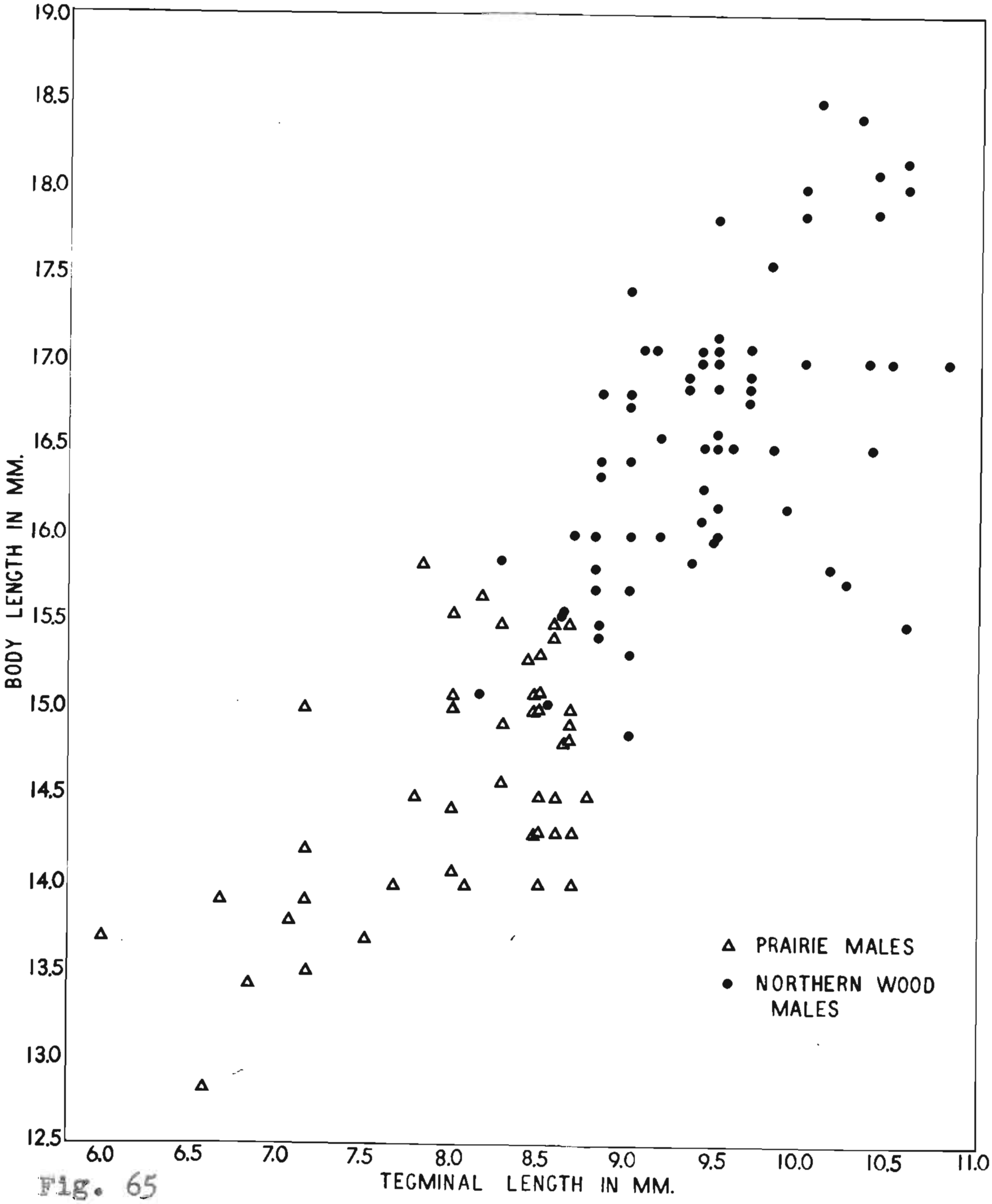


Fig. 65

the widest part of the pronotum generally near its anterior margin and the head as often wider than the pronotum as not. This character of proportionate width of head and pronotum readily separates the males of the prairie cricket and the northern wood cricket from the mountain cricket males without overlap.

With respect to coloration, the northern wood cricket represents an extreme, being nearly always totally black in color. A few specimens have reddish areas near the base of the hind femora. Mountain crickets vary from totally black specimens to specimens with small light spots on the sides of the pronotum and rather pale brown tegmina and hind legs. Beach, triller, southern wood, and prairie crickets are all somewhat paler. Beach and triller crickets often have light reddish margins on the pronotum, although some are nearly completely black. The males of both the prairie and the southern wood cricket can be separated from those of the northern wood cricket by color alone.

The northern wood cricket is the smallest of the six populations, with the smallest specimens seen only 12.8 mm. in body length (male), while the beach cricket is the largest with specimens up to 24 mm. (female) in the author's collection. Rehn and Hebard (1915, 26) list the range of body length for American Acheta as from 14.0 to 28.8 mm. The southern wood cricket and prairie cricket are slightly larger than the northern wood cricket, with considerable overlap, and the triller and the mountain cricket are smaller than the beach cricket. These two overlap considerably with the beach cricket in body length, but are fairly distinct from the prairie cricket and the southern wood cricket in this character. The triller averages slightly smaller than the mountain cricket, and the fall mountain cricket averages slightly smaller than the spring mountain cricket.

Several reasons for the confusion in early attempts to split this genus into species on the basis of morphological characters have already been mentioned. One of the most important of these is probably the disproportionate numbers of specimens collected of the different species. Lutz (1908, 26) placed great emphasis on the fact that the extremes of the characters he studied were represented in relatively few specimens, as one would expect in a single, highly variable population. He states, "Typical specimens of americanus (northern wood cricket) and firmus (beach cricket) are rare for the same reason that very short men and very tall men are rare." The present study indicates that they are rare in collections because of less likelihood of encountering them and greater difficulty in capturing them.

Crossing Experiments and Hybridization

The only evidence of hybridization of the northern crickets in the field, in spite of concentrated collecting along zones of contact and overlap, consists of one nymph collected in a field in southern Ohio which supports both prairie and mountain crickets. This individual, though having the narrow head and general body proportions of the prairie cricket, had long black tegmina and fully developed underwings, and was larger than any prairie cricket collected. His chirping had the typical regularity and speed of wing motion of the prairie cricket, but the chirps were four-pulse and delivered at a rate of about 240 per minute (80° F.). He failed to produce offspring when mated with a spring mountain cricket.

As shown in Plate XXXI, 30 crosses have been completed between Ohio, Indiana, and Illinois spring crickets. A total of 33 controls run concurrently produced offspring in 31 cases. A few crosses have been completed between northern and southern material. Two cases of hybridization have occurred between prairie and mountain crickets, and one between a northern wood female and a spring mountain male. In the crosses with Fulton's crickets, one beach x spring mountain cross has occurred, and the only southern wood x prairie cross attempted was successful. No hybrids were produced in nine attempts between the spring and fall mountain crickets, nor in nine attempts between prairie and northern wood crickets.

The three successful crosses indicated in Plate XXXI probably do not reflect a lack of reproductive isolation in the field. The prairie cricket and mountain cricket adults occur in the same places at the same time and yet maintain their separate identities. These crosses do indicate, however, that physiological isolation is incomplete, and that the effective isolating factors in the field are probably behavioral. This is strengthened by the fact that only one presumed hybrid has been heard or collected in the field. Song differences may be of importance in this regard, although tests have not yet been performed

PLATE XXXI. Fig. 66

CROSSING EXPERIMENTS WITH OHIO FIELD CRICKETS

FEMALES \ MALES	SPRING PASTURE	NORTHERN WOOD	PRAIRIE
SPRING PASTURE	●●●●●● ●●●●●● ●●●●○○	○○○○○○ ○	○○○○○
NORTHERN WOOD	●○○	●●●●●●	○○○○
PRAIRIE	●●○○○	○○○○	●●●●●● ●●●●

● OFFSPRING PRODUCED ○ NO OFFSPRING

to determine whether or not the observed differences in song are significant with respect to the behavior of the females.

In all possible types of matings between northern species, courtship, successful copulation (transference of the spermatophore), and oviposition occurred, though not in all the individual matings. In comparing crosses and controls, it was noted that in matings set up at the same time the above events appeared to take place sooner in the controls than in the crosses. Males in crosses were heard singing the solitary song much more frequently than those in control matings. This song is generally not produced in the presence of a responsive female. Adult females in cross-matings, and virgin females caged alone often chewed their way through the cheesecloth covers of the cages and escaped, while this happened only once or twice in control cages. This increased activity could have been due to attraction by the songs of males of their own species coming from other cultures in the room, or to some change in physiological condition.

Phylogenetic Implications

Our knowledge of the distributional and other relationships of *Acheta* populations is too scanty to allow any great amount of speculation as to their origin. However, the above comparison of morphological, ecological, song, and distributional relationships, suggests some historical aspects which are worthy of mention.

Three of the crickets under consideration have the ability to produce long-winged individuals (mountain, triller, and beach), two do not (northern wood and southern wood), and one apparently does so very rarely (prairie). Wing reduction here is probably a secondary condition, and it is logical to assume that the short-winged forms are descended from a population with the ability to form long wings.

The mountain cricket and the triller have both spring and fall representatives. Of the other four populations, three are spring crickets, and one is a fall cricket. Both the mountain cricket and the triller exhibit considerable variation with respect to all characters studied, while at least three of the others are quite uniform.

From these comparisons we might speculate that the common ancestor of all these populations was a double-brooded cricket occurring in pioneer associations and possessing the ability to produce long-winged individuals.

As pointed out to the writer by Dr. Fulton, in this genus, as well as in others, those species occurring in pioneer associations are generally able to develop long-winged individuals, while those occurring in mature or climax associations are generally not able to do so. A point of interest is that the prairie cricket is somewhat intermediate in this respect. No long-winged forms have ever been taken in the field, and the "long wings" developed in the laboratory were not as long as those developed in the beach, triller, and mountain crickets. They extended scarcely beyond the tips of the tegmina, and it is doubtful if their possessors were capable of flight.

This may be correlated with the relative recentness of the prairie habitat in Illinois, Indiana, and Ohio, and its somewhat intermediate position with respect to stability and permanence there. The "prairie-like" Andropogon-covered hillsides in southeastern Ohio are a sort of "long stage" in the succession, sometimes requiring 20-40 years to become overgrown with sumac, pine, dogwood, and finally oak forest.

It is possible to speculate upon the changes that settlement and clearing have brought about with respect to the relative numbers and the type of distribution of the field crickets in Ohio, Indiana, and Illinois. Prior to settlement, about 95% of the state of Ohio was forested and 5% was prairie. Today, only 5% of the state is forested, and the rest is involved in agriculture and perpetually in various types of grassy, weedy, or cultivated situations. Today the range of the mountain cricket is fairly continuous across Ohio, Indiana, and Illinois, while the northern wood cricket and the prairie cricket occur only in small, isolated colonies. The uniformity of these last two species across a range of 300-400 miles from east to west suggests, however, that their distribution was once fairly continuous, and for a relatively long period of time. It is probable that the wood cricket was once the dominant species in this area, and the prairie cricket must have occurred continuously across the southern half of these states. The mountain cricket may not have even entered this heavily forested area before settlement, and at any rate it did not have a continuous distribution as it does now. In unsettled areas in the Appalachian Mountains this cricket occurs in areas cleared by rockslides.

Acheta domesticus Linnaeus

The European House Cricket

Distribution

This species, introduced from Europe, apparently occurs all over Ohio, Indiana, and Illinois, though I have never found it in large numbers in any location. It is probably the only singing insect which can be heard in downtown areas of large cities, with the possible exception of the cicada, *Tibicen linnei* (S. and G.), which I have heard singing from utility poles in downtown Columbus, Ohio. In Columbus I have heard the house cricket in warehouses, store basements, and greenhouses in summer and winter, and along sidewalks and under buildings in summer.

Singing Behavior

The house cricket is the only singing insect in Ohio which can be heard all winter long (inside buildings and in warm places). It sings both day and night, but chiefly at night.

The situations in which this species produces sounds, and the modifications in the sounds produced in these situations are practically identical to those described for *Acheta assimilis* (mountain)(p. 98-105). In short, in addition to the well-defined calling and courtship songs, a male cricket in a culture or cage chirps almost every time he encounters another cricket, male or female. These chirps vary from one situation to another, and with a little practice each type of chirp can be recognized by ear. Sometimes only a slight movement on the part of a nearby individual is sufficient to alter the chirping of a male sufficiently for human ears to detect the change. The behavioral significance of such slight alterations, if any, remains to be demonstrated.

Song Description and Analysis

The calling song at 80° F. is a more or less continuous succession of three-pulse chirps at about one per second, with the wing-stroke (pulse) rate about 16 per second (Plate XXVI). The sound pulses are dominated by a pure tone pitched at about 4000 cycles per second and each pulse is downslurred across about 200 cycles per second during its length of 20-30 milliseconds. The first pulse of a chirp is usually shorter than the others. The tegmina are held at about a 45° angle during the calling song.

The only other steady, consistent singing of this species is its full courtship song which consists of 8- to 12-pulse phrases or chirps at 15-20 pulses per second, each phrase terminated by a high-pitched and relatively loud pulse, slightly separated from the rest of the phrase (Plate XXXIV). The pulse rate decreases toward the end of the phrase, varying from 20 to 12 pulses per second within each phrase. The phrases are produced at a rate of about 2 per 3 seconds. This sound is not dominated by a pure frequency as is the calling song, and is very soft and "noise-like," with a wide frequency spectrum. The tegmina are scarcely lifted at all, but are tilted roof-like over the abdomen, and the male jerks his body continually and backs toward the female, terminating the song only when she leaves, or copulation is effected.

The chirps which are emitted in encounters with both male and female crickets, and in courtship interruption, or departure of the female from a courting male, are, as in the field crickets, characterised by being long (many-pulse), loud, and clear, and seemingly occurring as individual units, rather than as parts of uniform sequences of chirps or phrases, or "songs." Such chirps may contain up to 25-30 continuously delivered pulses. The rate of wingstroke, as in the courtship phrases, is usually more rapid in the first part of the chirp, decreasing toward its end, varying from 20 to 12 per second in the same chirp. Downslurring is particularly evident in the pulses of these chirps.

The transition from calling song to courtship song by a male approached by or approaching a female, often involves, as in the field crickets, long sequences of one- or two-pulse, rather soft and non-musical chirps (pre-courtship). Eventually this passes into the mixed courtship singing which is characterised by containing the characteristic rhythm of the courtship song, but is interspersed with clear, loud pulses such as are produced during the calling song. Again, as with the field crickets, a slight withdrawal of a female from a courting male may cause an increase in the proportion of clear, loud pulses in the mixed courtship singing, and an increase in responsiveness, or a failure to withdraw from a courting male, causes a reduction in the number of such pulses, or their complete disappearance from the courtship song. Mixed courtship singing may go on for several minutes if a female remains near a courting male, but fails to mount him or allow him to back under her. The full courtship song is rarely produced for such long periods of time. If a female fails to respond to a male giving the full courtship song, he will usually either change over to mixed courtship singing, or give the loud, long chirp of courtship interruption, turn around and "caress" the female with his antennae, then begin courtship singing all over again, usually with mixed courtship singing.

Male house crickets commonly court each other and nymphs of both sexes, and one male was seen to "court" the corner of a cage, eventually backing against the wall and rubbing a spermatophore off against it. On another occasion a virgin male that had been caged alone for several weeks of his adult life was observed singing a mixed courtship song in the middle of a culture jar, and was rubbing his abdomen against the sand on the bottom of the cage. A male field cricket collected in the field and held inside my hand for want of a better container, sang what sounded like a mixed courtship song while inside my fist. These observations would indicate that courtship singing may be induced by odor alone, or by the sight and/or smell and touch of another cricket, whether male, female, or nymph. At the time the field cricket sang in my closed fist, I had been handling field crickets all day in the laboratory.

The above observations were all carried out on house crickets from a culture obtained from the University of Missouri.

The calling song of this species has been described and analyzed by Pierce (1948, 26) who states that it consists of 3-pulse chirps with chirp intervals irregular, but averaging 0.67 second, and the duration of each pulse being about 0.03 second. He gives the dominant frequency as 3800 cycles per second, and his diagram indicates a pulse rate of about 14.6 per second. Busnel (1953, 6) determined the dominant frequency in this song to be 4500 cycles per second, plus or minus 500 cycles per second, due to individual variation.

Pierce (1948, 26) says the courtship song of this species "...con-sists of a continuous trill at about F = 9000, and occasionally of chirps at F = 24,000."

Diagrammatic drawings of the file and scraper of this species are shown in Plate IV. The file is about 2 mm. long, with about 40 teeth per mm. near the center. The teeth are smaller and more closely spaced toward either end of the file.

<u>Miogryllus verticalis</u> (Serville)

Serville's Ground Cricket

<u>Distribution</u>

In central Ohio this species extends only as far north as southern Fairfield County, but in Illinois it is abundant in northern Piatt County, and was collected by E. L. Sleeper at a light in McLean County in June, 1954. In eastern Ohio it extends at least to Coshocton County. It is commonly encountered in pastures, weedy areas, and along roadsides and fencerows, especially in well-drained situations. In southeastern Ohio it is characteristic of the _Andropogon virginicus_-dominated, abandoned field situations, and in southwestern Ohio and southern Illinois it also occurs in the hill prairie openings which are generally dominated by _A. scoparius_. In both areas this cricket and the prairie _Acheta_ occur together.

In southeastern Ohio this species has been heard from June 4 until July 17. Isely (1905, 26, Kansas) found adults on May 22 and found none after June 23, though he found specimens of a pale form, previously known as _M. saussurei_ Scudder, and placed in synonymy by Hebard (1915, 26), on August 8.

Blatchley (1920, 6, Indiana) found this species on dry, wooded hillsides in the southern third of the state and states, "It seems to like best places devoid of grass and other vegetation." Isely (1905, 26) found it especially abundant in thick, short, dead grass on a hillside in Kansas.

Singing Behavior

This species produces the calling song both day and night, but at any given time during the night, more individuals will be singing simultaneously than at any time during the day, as with most of the Gryllinae.

Laboratory observations on this species indicate that it possesses the same sound responses as have already been described for *Acheta*, including well-defined calling and courtship rhythms, and the distinctive chirps produced during encounters with males, with females, and upon interruption of courtship.

Song Records[2]

*Piatt Co., Ill., (Sangamon Twp.) 16 June 1954, 80° F., 96 chirps/ 58 sec.

*Adams Co., O., (Jefferson Twp.) 9 July 1954 (temp. unk.), 50 chirps/30 sec.

*Adams Co., O., (Meigs Twp.) 8 June 1955 (temp. unk.), 32 chirps/48 sec.

*Vinton Co., O., (Lake Hope) 17 June 1954, 85° F., 142 chirps/ 2 min. and 4 min., "fight" song and courtship song, all in the laboratory.

Hocking Co., O., 4 June 1955, Perry Co., Ill., 15 June 1955, Cairo, Ill., 16 June 1955, Licking Co., O., 17 July 1955, Coshocton Co., O., (Jefferson Twp.) 11 July 1954.

Song Description and Analysis

The calling song is a continuous succession of soft, high-pitched buzzy-sounding chirps repeated at a rate of 1-2 per second

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2. This symbol (*) indicates that the reference is to a tape recording. Song records without this symbol are "listening" records. Numbers in parentheses listed under a single locality refer to recordings made of different individuals. If date, and/or temperature are not listed for each individual, this means that this information is the same as that already given for the previous individual.

between 70° F. and 80° F. It is audible only a few yards away, and to the ear differs from the calling song of Nemobius socius only in the slower chirp rate. Each chirp contains about fifteen pulses at a rate of 120-125 per second, and is pitched at around 6 kilocycles per second (Plate XXXII). The dominant sound is not as pure in frequency as in the calling songs of Acheta.

When two males of this species encounter each other, they emit the long chirps shown in Plate XXXII (male encounter), containing up to 30 or 35 pulses. The same type of chirp is produced when a female is encountered. As in Acheta, the rhythm of the calling song is broken with the production of such chirps, and each chirp seemingly becomes an individual unit. Several may be produced in rapid succession, or one may be produced alone, depending on the situation. If one of two encountering males does not leave immediately, a number of such chirps will be produced, probably by both individuals, and a fight may occur.

The courtship singing of this species involves an increase in chirp rate and a decrease in the number of pulses per chirp, as shown in Plate XXXII. The extreme noted in this trend was a chirp rate of 7-8 per second with each chirp containing 7-8 pulses. A great deal of transitory singing occurs which is intermediate between the calling song and the courtship song.

The calling song of this species has been described by the following authors:

Allard (1911b, 6, Thompson's Mills, Ga.), 38-39 "trills"/min.

PLATE XXXII SOUNDS OF MIOGRYLLUS VERTICALIS

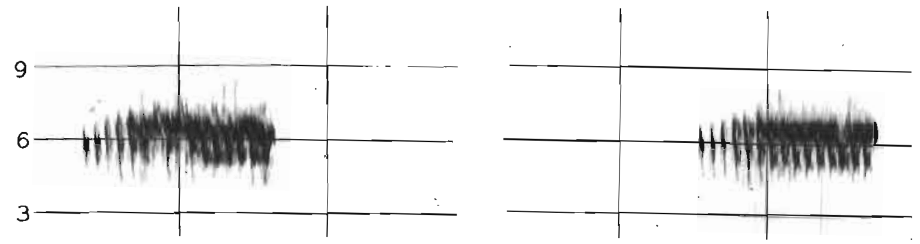


Fig. 67. CALLING SONG

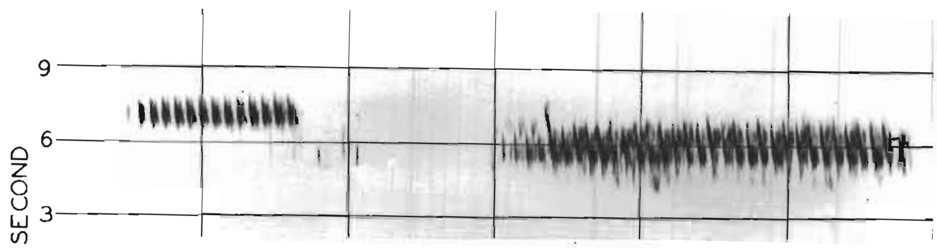


Fig. 68. MALE ENCOUNTER
(HERE WITH NEMOBIUS SOCIUS)

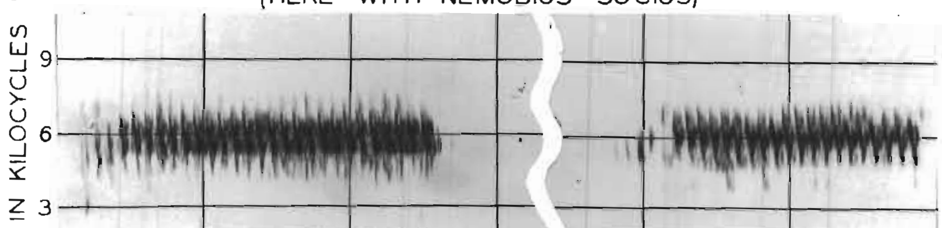


Fig. 69. FEMALE ENCOUNTER

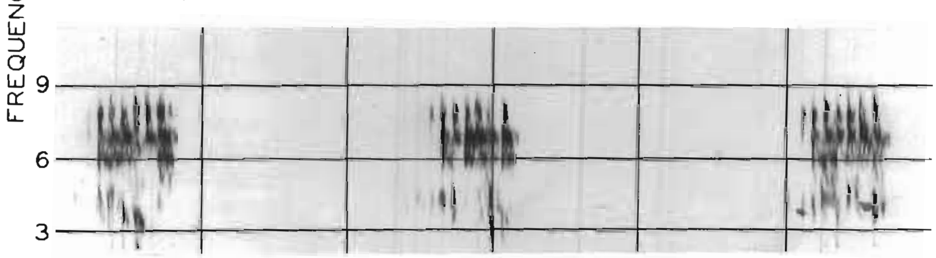


Fig. 70. TRANSITORY TO COURTSHIP

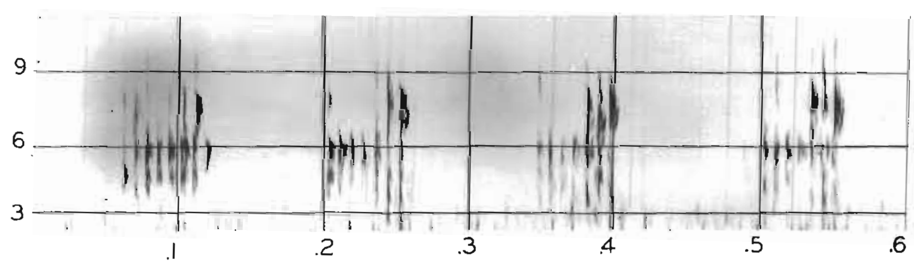


Fig. 71. COURTSHIP SONG
TIME IN SECONDS

Fulton (1932, 6, North Carolina), 6-11 notes in 10 sec.
Allard (1928a, 6) 38-40 chirps/min.
Davis (1909, 6, New Jersey) "...a slow see, repeated at intervals of several seconds."

These descriptions seem to largely agree with that given here.

Gryllodes sigillatus (F. Walker)

The Decorated Cricket

This species is known to me only from several specimens obtained from the Melton Cricket Hatchery in Etna Green, Indiana, where they were obtained in a shipment of *Acheta* from Florida and are being reared continuously for sale as fish bait. Only the calling song and the courtship song were observed in the two specimens obtained.

Song Description and Analysis

The calling song of this cricket is a continuous succession of 4-pulse chirps with a chirp rate of 5-6 per second and a wingstroke rate of 50-60 per second at 80-85° F. (Plate XXXIII). It sounds very much like the song of the prairie *Acheta* or the southern wood *Acheta*, but is slightly higher-pitched, and the chirp is 4-pulse rather than 3-pulse as in these species of *Acheta*. It is not a very musical chirp, and it is rather soft when compared to the songs of the various species of *Acheta*.

The only other song observed for this species was apparently the full courtship song (Plate XXXIV), consisting of phrases produced at a rate of about 2 in 3 seconds and containing about 7, 3- or

PLATE XXXIII. CALLING SONGS OF CHIRPING CRICKETS

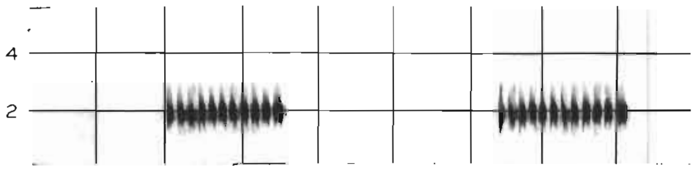


Fig. 72. GRYLLOTALPA HEXADACTYLA

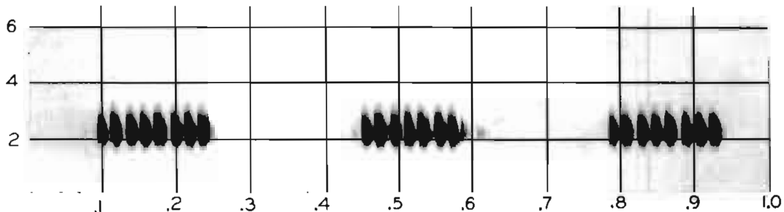


Fig. 73. OECANTHUS NIVEUS

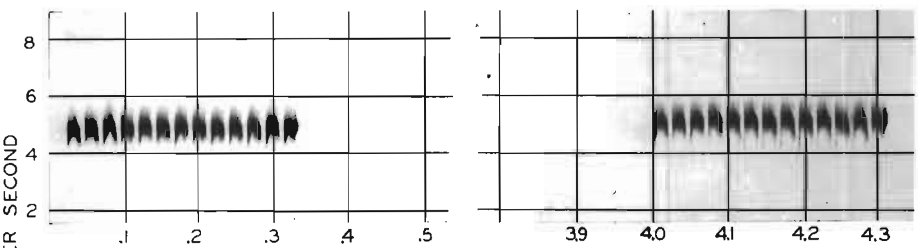


Fig. 74. OROCHARIS SALTATOR

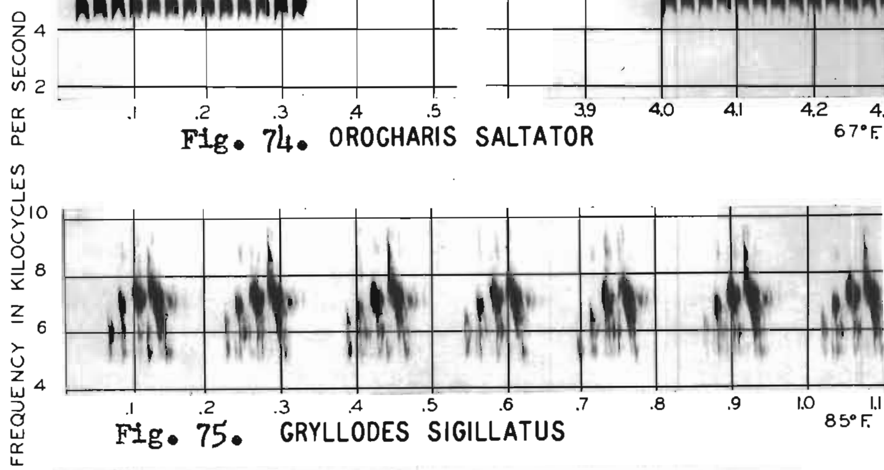


Fig. 75. GRYLLODES SIGILLATUS

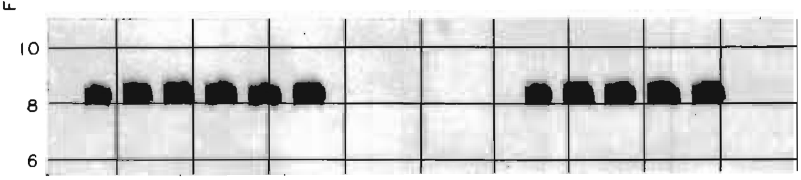


Fig. 76. CYRTOXIPHA COLUMBIANA

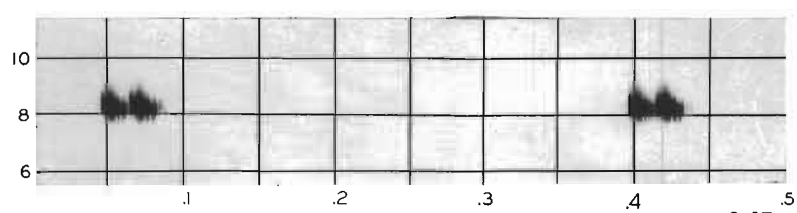


Fig. 77. CYCLOPTILUM BIDENS

TIME IN SECONDS

PLATE XXXIV.

COURTSHIP SONGS OF SOME GRYLLINAE

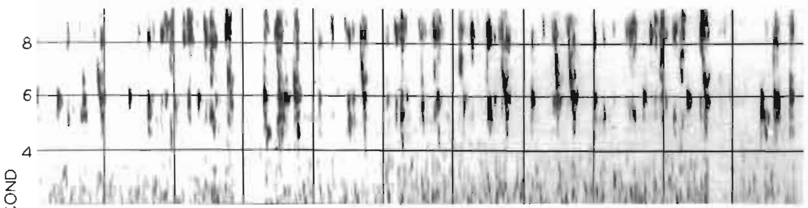


Fig. 78. GRYLLODES SIGILLATUS

Fig. 81. BEACH ACHETA

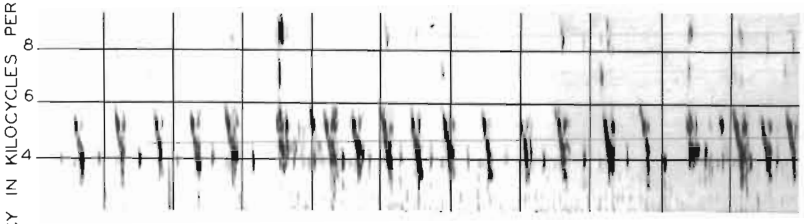


Fig. 79. ACHETA DOMESTICA

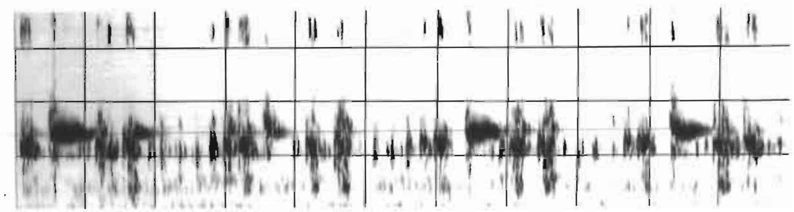


Fig. 82. NORTHERN WOOD ACHETA

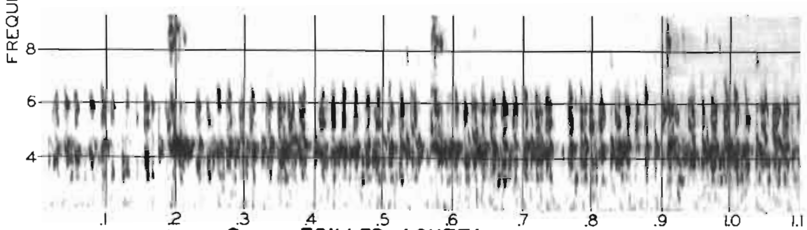


Fig. 80. TRILLER ACHETA
TIME IN SECONDS

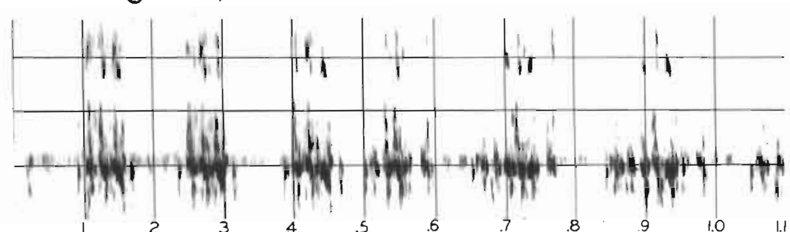


Fig. 81. PRAIRIE ACHETA
TIME IN SECONDS

80-85°F.

4-pulse phrases slightly separated from each other. The whole phrase terminates in a louder, sharp pulse, much like those in the courtship songs of the various species of *Acheta*. Like the courtship songs of *Acheta*, this courtship song is much softer than the calling song, and as shown in the Vibragram, seems to scarcely emerge from the background noise.

The song of this species has been referred to by Hehn and Hebard (1907, 6, Miami, Florida) as, "...a shrill sound easily distinguished from that of *Gryllus luctuosus* by its higher pitch and the longer duration of its stridulation." This does not sound like the song described above, but is difficult to compare with it.

The *Nemobius fasciatus* Group

Nemobius fasciatus (DeGeer), *N. tinnulus* Fulton, and *N. socius* Scudder are treated in this paper as distinct species. They are most often called subspecies, in spite of the fact that their geographic ranges are not greatly different, and frequently *socius* and *fasciatus* occur together in the same habitat. Fulton (1933, 6, and 1937, 6) was unable to get *socius* to cross with either of the other two, though he got fertile hybrids in crosses between *fasciatus* and *tinnulus*. No one has ever reported hearing an intermediate song in the field, such as Fulton's hybrids produced. Therefore, it seems that these three forms cannot be regarded as anything other than distinct species, as was pointed out by Mayr (1948, 26).

Fulton's (1933, 6) description of the ecological relationships of these three crickets is as follows; "Socius is a grassland race occurring in greatest numbers in moist meadows and marsh borders. In the northern states it is confined to low ground, but in the south it is more widely distributed. Tinnulus is a woodland race living in the less densely shaded types of developmental or sub-climax forest. In respect to habitat also [referring back to morphology] fasciatus is intermediate between the other two races. It is associated with grass, but may live in open woodland or under trees where there is enough light to permit a good growth of grass."

Cantrall (1943, 6, George Reserve, Michigan) found the ecological distribution of these three species in agreement with Fulton's generalizations. He found colonies of fasciatus and tinnulus only ten feet apart.

My observations on the ecology of these three species in Ohio, Indiana, and Illinois, agree with those of Fulton. Fasciatus and socius are found mixed together, sometimes in colonies of great density, seemingly as often as they are found in separate colonies. Tinnulus is characteristic of the rather open oak forests along the ridgetops in unglaciated Ohio; on one occasion a single specimen of fasciatus was heard singing from under the stone steps of an old cabin halfway up a wooded slope supporting a colony of tinnulus. In Franklin and Williams Counties, Ohio, tinnulus was heard in leaf litter along dense forest borders and in open second-growth timber.

Nemobius fasciatus (DeGeer)

The Striped Ground Cricket

Singing Behavior

The striped ground cricket sings day and night from late June until after the first heavy frosts in the fall at Columbus, Ohio. When the other singing insects have been annihilated by the first heavy frost, the high-pitched, inconspicuous song of this species becomes suddenly very noticeable, the combined songs of hundreds of individuals in a lawn fairly making the air ring. Early in the season it seems to sing more at night than by day, but in fall when the temperature drops to below 50° F. shortly after dusk, the greatest part of its singing is done during the warm part of the day.

In addition to the calling song, several courtship rhythms have been observed in this species. Sufficient observations have not been carried out to determine whether or not specific responses occur in other situations as they do in the field crickets.

Song Records

The calling song of this species has been heard in almost every locality visited during the two years of this study.

*Franklin Co., O. (Clinton Twp.) (1) 24 July 1954, 62° F., 34 sec., 10.8 pulses/sec. (2) 45 sec., 10.8 pulses/sec. (3) 35 sec., 11 pulses/sec. (4) 38 sec., 11.2 pulses/sec. (5) 29 June 1954, approx. 75° F., 14 pulses/sec. (6) 19 July 1954, 85° F., 2 min. 35 sec., 17.6 pulses/sec. (7) 5 July 1954, 90° F., 3 min. 10 sec., 18 pulses/sec. (8) 15 sec., 80° F., 17.2 pulses/sec. (9) 25 Sept 1954 , 80° F., 90 sec., 17.2 pulses/sec. (10) 28 July 1954, 70° F., 65 sec., 14.4 pulses/sec. (11) 72° F., 60 sec., 13 pulses/sec.

*DuPage Co., Ill. (Bemis Woods) 70° F., 45 sec. 12 pulses/sec. in calling song and 5-7 pulses/sec. in courtship song.

*Hocking Co., O. (Neotoma) 4 Sept 1954, about 85° F., 60 sec., 18 pulses/sec.

*Piatt Co., Ill. (Sangamon Twp.) 5 Sept 1955, 58° F. 90 sec., 9 pulses/sec.

Song Description and Analysis

The calling song is a series of clear, high-pitched, tinkling trills, each lasting from 2-15 seconds, rarely longer, with the individual pulses delivered at rates varying from 9 to 18 per second between 58° F. and 90° F., as shown above. The breaks between trills are only a fraction of a second in length. At 80-85° F. the dominant frequency in the song is around 7500-8000 cps.

Like *N. tinnulus*, this species has 3 courtship rhythms. In the early stages of courtship when the male is still facing the female, he produces trills 1-2 seconds in length, the pulses delivered at the same rate as in the calling song, with each trill followed by one pulse a little separated from the rest, then a half second rest before the next trill. As this song is produced the male jerks his body backward each time the disjunct pulse is produced at the end of a trill. This is probably analogous to pre-courtship in the *Acheta* and *Miogryllus*. When courtship has seemingly advanced somewhat, and the male reverses his position and begins to back toward the female's head, a slower pulse rate of 5-6 pulses per second is produced, and the pulses are grouped 4-8 in a series with breaks of a fraction of a second between series. Sometimes this song develops into a uniform slow tinkle, like the solitary song of <u>tinnulus</u>, without the pulses being grouped at all. In these two songs, the male jerks his body each time a group of pulses is produced, or "shudders" rapidly during the ungrouped pulse sequence. The ungrouped, slow pulse-sequence is probably analogous to full courtship in the <u>Acheta</u>, and the intermediate rhythm to the mixed courtship of <u>Acheta</u>.

The solitary and courtship songs of this species have been described or analysed by the following authors:

Morse (1920, 6) New England.
Fulton (1931, 6, 1933, 6) Iowa, Raleigh, North Carolina and western (mountainous) North Carolina.
Cantrall (1943, 6) George Reserve, Michigan.
Pierce (1948, 6) Franklin, New Hampshire.
Pielemeier (1946, 26) University Park, Pennsylvania.

Fulton's estimates of the pulse rate are as follows: Iowa, 5-6/sec. at 50° F., 8-9/sec. at 61° F.; North Carolina Mts. 7/sec. at 60° F., 8/sec. at 66° F., 9/sec. at 68° F., "Specimens from Raleigh, North Carolina appear to have a slightly higher rate than the mountain specimens." In 1933 he gave the range of pulse rate in this species from 5½/sec. at 50° F. to 15/sec. at 80° F.

Fulton also describes two variations of the "mating" (courtship) song. "When a male is facing a female it sometimes sings... in short phrases about one and one-half to three seconds duration, with rests of about half a second. At other times the male chirps louder and at a much slower rate, about 5 or 6 per second, without regular rhythm and accompanies some of the notes by jerks of the body backward and forward."

Cantrall described a possible mating or courtship song unlike those noted above, and apparently similar to the courtship song in *Acheta* and *Gryllodes*. "The tegmina were held in singing position and were shuffling as though in normal song, but I could hear only an occasional 'teek' (4 in 45 sec.)." Cantrall observed this song in a lone male bearing a spermatophore and apparently very "excited," then in the same male after he had eaten the spermatophore and a female had approached. This is a very interesting observation, since courtship songs similar to those of other Gryllinae had not been previously noted in *Nemobius* species.

Pierce noted pulse rates varying from 14.5 to 20 per second in this species, at temperatures ranging from 69.4° F. to 96.8° F. He gives the dominant frequency in a song delivered at a rate of 19 pulses per second, as 7500 cps.

Pielemeier gave a pulse rate of 20 per second for this species, and found intensity peaks in the frequency spectrum at 8.3 kilocycles per second, (61 decibels at 1 foot), 17.4 kps. (35 db. at 1 foot), and 28 kps. (48 db. at 1 foot).

Nemobius tinnulus Fulton

The Tinkling Ground Cricket

Singing Behavior

The tinkling ground cricket sings day and night from around mid-July to at least mid-September at Columbus, Ohio. Cantrall's last record on the George Reserve, Michigan, was on September 23, but he believes adults could probably be found "until sometime in October." Fulton (1932, 6) gives the seasonal song period at Raleigh, North Carolina, as from early August to December 1.

In addition to the calling song, two distinct courtship rhythms have been observed in caged specimens of this species. Sound production has not been observed in other situations.

Song Records

*Hocking Co., O., Neotoma, 3 Sept 1954, 63° F., 153 pulses in 30 sec (5.1/sec.).

*Hocking Co., O., Goodhope Twp., 15 Aug. 1955, 85° F., 68 sec., 10 pulses/sec.

*Vinton Co., O., Lake Hope, 20 Sept 1954, 80° F., 1 min. 55 sec., 944 pulses (8.1/sec.).

*Carroll Co., O., 14 Aug. 1954, 80-85° F.

*Porter Co., Ind., Dunes Park, 19 Aug. 1954, 80-85° F.

Franklin Co, O., Blendon Twp., Aug-Sept 1955, Ashland Co., O., Mohican State Forest, 26 Jul 1955, Raleigh, North Carolina, 9 Aug 1955.

The calling song is a continuous succession of high-pitched (8.5-9 kps.), clear, sharp pulses repeated at rates of 5-10 per second at from 60-85° F. (Plate XXXV). As shown in the graphs the intervals are much longer than the pulses themselves which last only about 30 milliseconds. In this type of trill, the wings are apparently held motionless between the strokes producing the sound pulses rather than being constantly opened and closed as in the

PLATE XXXV. SUBSPECIES OF NEMOBIUS FASCIATUS

FASCIATUS

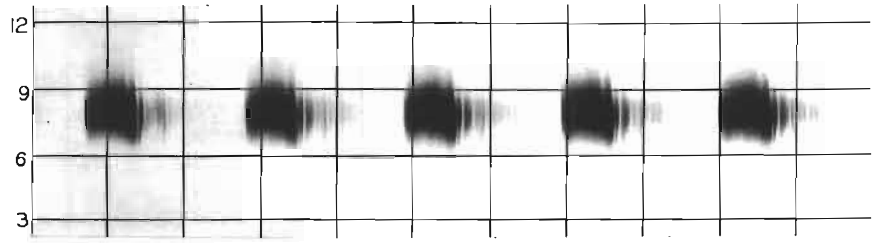


Fig. 84. SOLITARY SONG

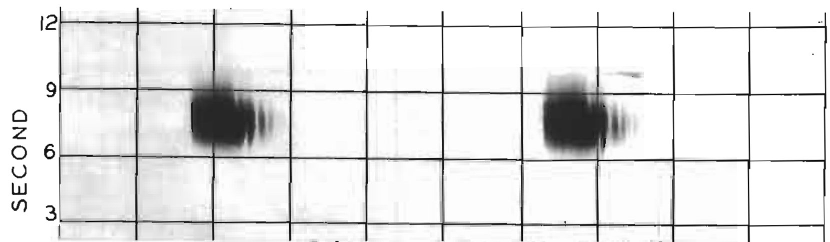


Fig. 85. COURTSHIP SONG

TINNULUS

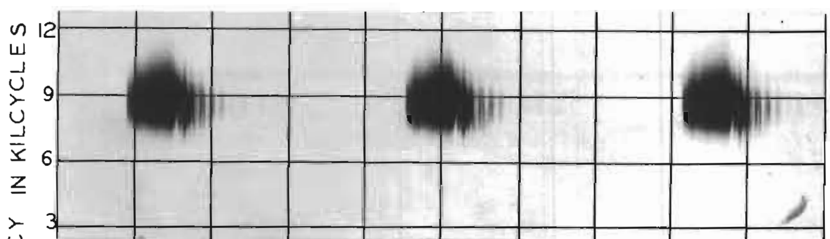


Fig. 86. SOLITARY SONG

SOCIUS

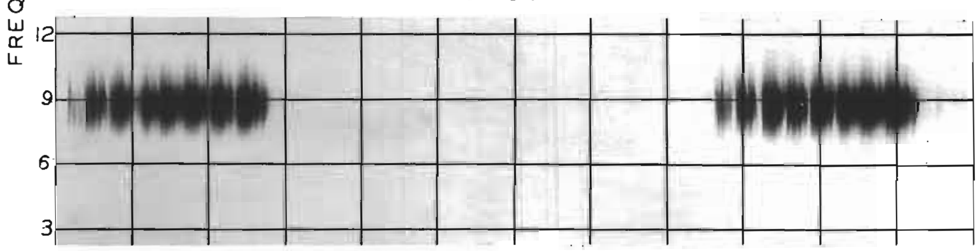


Fig. 87. SOLITARY SONG

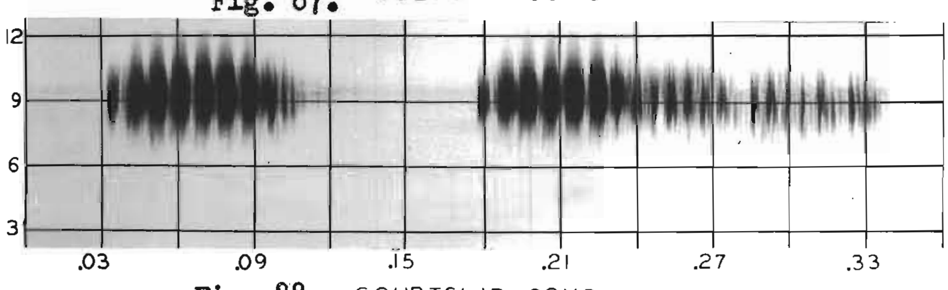


Fig. 88. COURTSHIP SONG
TIME IN SECONDS

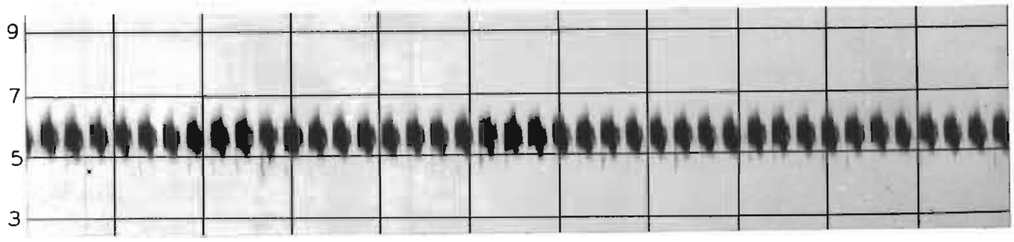
trills of tree crickets, and other species of *Nemobius* (Plates XXXVI, XXXVII). This is also true in the song of *N. fasciatus*, but is less obvious because of the faster pulse rate. The speed of wing motion in *tinnulus* and *fasciatus* is apparently about the same, with only the length of the interval between sound pulses, or the time during which the wing is held motionless, varying.

The calling song of this species is only audible a few yards away, and at night is almost completely obscured by the louder insects.

The courtship singing has not been recorded (on tape), but a cage containing males and females was kept on my desk for several weeks, during which time several courtship sequences were observed. Two different rhythms are produced at different stages of courtship. When a male has just approached a female and is still facing her, he delivers pulses at the rate of about 2-3 per second, and groups them in sets of 2-4, with a slightly longer interval between groups. After each group of 2-4 pulses, he jerks the body backward slightly in the manner characteristic of courting male crickets. Eventually the male reverses his direction, stops jerking, and backs toward the head of the female, while producing a regular succession of pulses at a rate of about 3 per second. During this sequence his body is "shuddering" as was described earlier for *N. fasciatus* in full courtship. This shuddering seems to occur at the same rate as he is delivering sound pulses. This is the courtship song most often heard from a culture, probably because more time is spent in this

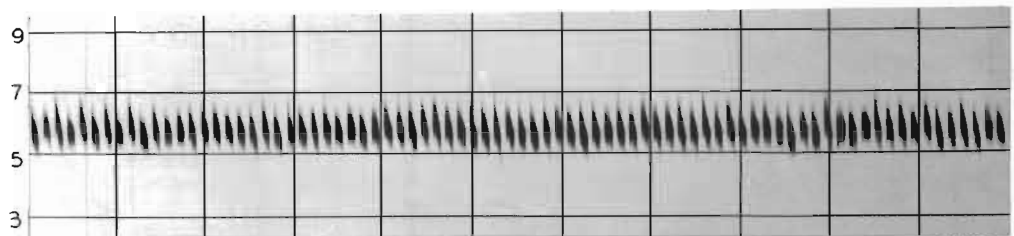
PLATE XXXVI. CALLING SONGS OF TRILLING NEMOBIUS

FREQUENCY IN KILOCYCLES PER SECOND



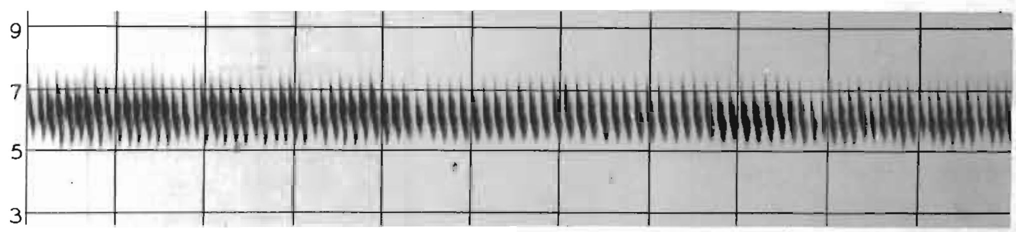
85° F.

Fig. 89. NEMOBIUS PALUSTRIS



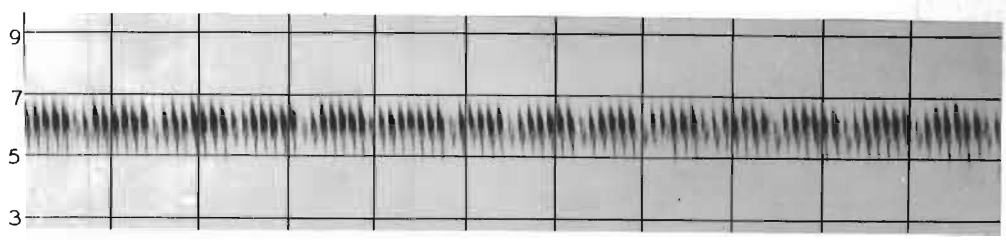
75° F.

Fig. 90. NEMOBIUS CAROLINUS (NON-PULSATING)



90° F.

Fig. 91. NEMOBIUS CAROLINUS (ALTERNATELY PULSATING)



90° F.

Fig. 92. NEMOBIUS CAROLINUS (PULSATING)

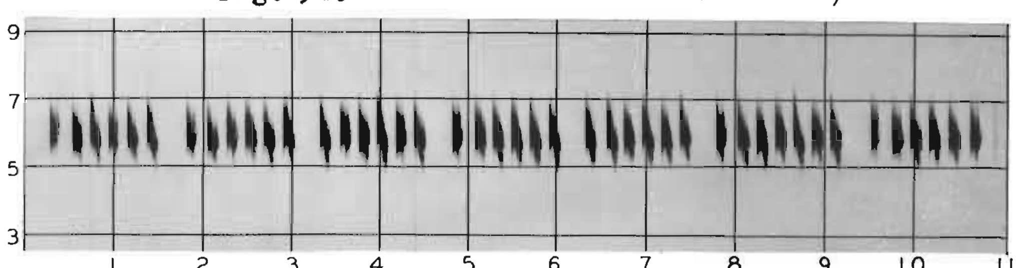


Fig. 93. NEMOBIUS MACULATUS

85° F.

TIME IN SECONDS

PLATE XXXVII. CHIRPING SONGS OF NEMOBIUS

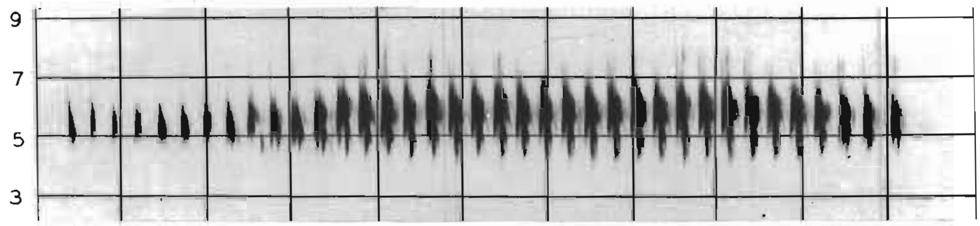


Fig. 94. NEMOBIUS CAROLINUS OR PALUSTRIS (COURTSHIP) 85°F.

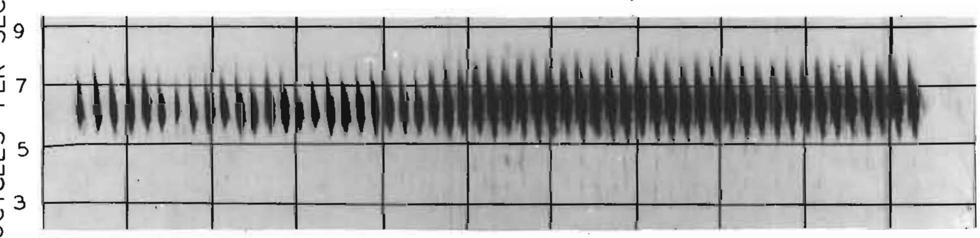


Fig. 95. NEMOBIUS CONFUSUS (CALLING) 85°F.

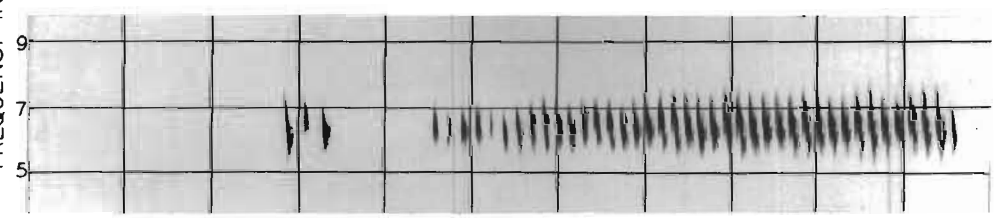


Fig. 96. NEMOBIUS CONFUSUS (CALLING) 85°F.

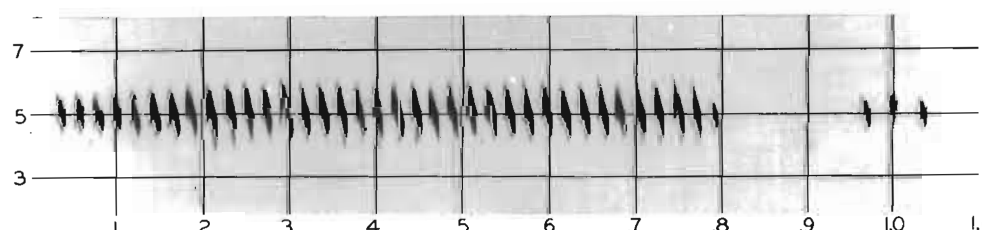


Fig. 97. NEMOBIUS CONFUSUS (CALLING) 65°F.

relationship than in the other, perhaps more preliminary phase of courtship. In some cases a male singing the calling song is approached from the rear by a responsive female, and the less common rhythm is completely omitted.

The analogous modification of the song from calling to courtship in the two species, N. fasciatus and N. tinnulus, is especially interesting in view of the relationship between their songs, and the results obtained by Fulton in crossing the two species. In both species the main courtship song is simply a slowed-up version of the calling song. In both species there are two courtship rhythms, which are related in the same way to the calling song and to each other. The full courtship song of fasciatus is practically identical to the calling song of tinnulus.

In all these variations, the only thing that changes is the length of the interval between pulses, during which the wings are held motionless. Fulton (1933, 6) crossed fasciatus and tinnulus and found that the resulting hybrids had pulse rates (or wing "hold" intervals) intermediate between those of the two parents. Backcrosses with the two parents moved the pulse rate toward that of the parent. Fulton concluded that the length of this interval seemed likely to be controlled by two or more determiners.

The relationship between the courtship song of fasciatus and the calling song of tinnulus is similar to that occurring between the courtship chirps of N. carolinus and N. palustris, and the calling songs of N. confusus and N. sparsalus (see Fulton, 1930-1931 for song description).

The calling song of this species has been described or analyzed by the following authors:

Allard (1910d, 6, Thompson's Mills, Georgia). The song was described under N. canus Scudder which was later found to be a synonomy of N. socius Scudder (see Hebard, 1913, 26), but the habitat and song given indicate that Allard was referring to tinnulus (described by Fulton, 1931, 6). "I find this large and active Nemobius only in the dry leaves of upland woods. The song ...is a high-pitched, tinkling trill — ti-ti-ti-ti-ti-ti-ti, prolonged indefinitely...day and night..."

Cantrall (1943, 6, George Reserve, Michigan) says the song is identical with that of Fasciatus except that the notes are given only about one-half as fast.

Fulton (1931, 6, Mt. Pleasant, Iowa) gives the following pulse rates: 7 and 8/sec at 80° F., 5 and 5.7/sec at 66° F., 4.4./sec at 65° F., 4.3 and 5/sec at 61° F., 3.8/sec at 59° F.

Fulton (1931, 6, Raleigh, North Carolina) gives the following rates: 7/sec at 82° F., 8/sec at 79° F., 7/sec at 75° F., 6/sec at 69° F., 5.5/sec at 67° F., 5/sec at 66° F., 4/sec at 60° F. (Mountains of North Carolina) 7-8/sec at 80° F., 5/sec at 66° F. "In the mating song the notes are sounded at about half the above rate, less rhythmically but sharper and more emphatically."

Pierce (1948, Franklin, New Hampshire) gives the pulse rate as 5-10 per second, with the dominant frequency of the sound at 6.3 kps.

at a pulse rate of 5 per second. This frequency varies somewhat with that obtained here.

Nemobius socius Scudder

The Marsh Ground Cricket

Singing Behavior

The marsh ground cricket sings day and night from early July until after the first heavy frosts at Columbus, Ohio.

Cantrall (1943, 6) found this cricket adult between July 20 and October 14 on the George Reserve, Michigan, and believes it to be single-brooded there, though Fulton (1933, 6) found it to be double-brooded in North Carolina.

A well-defined courtship rhythm and a "male encounter" chirp have been observed in this species, in addition to the calling song.

Song Records

The calling song of the marsh ground cricket has been heard continuously from early July until heavy frost at Columbus, Ohio; it was heard at nearly every locality visited during this study. The following recordings were made:

*Adams Co., O., Jefferson Twp., 10 July 1954, 80° F. (1) 60 sec (several males singing at once) (2) 70 sec (3) 2 min. 55 sec (4) 4 min. 33 sec.

*Licking Co., O., Cranberry Bog on Buckeye Lake, 25 Sept 1954, 80-85° F., 23 sec.

*Bourbon Co., Ky. (Walker), 14 July 1955, 20 sec.

Song Discription and Analysis

The calling song is a continuous repeating (at 2-3 per second, and not at a uniform rate) of high-pitched, soft, buzzy, multi-pulse chirps, each lasting a little less than a tenth of a second. The dominant frequency in the sound is between 9 and 10 kilocycles per second, and the pulse rate is around 100 per second at 80° F. The song is audible only a few yards away. Each chirp contains 7 or 8 pulses (Plate XXXV).

In the courtship song of this species, the chirps are grouped in two's and three's (rarely larger groups), with the last chirp in each group a little longer and its pulse rate a little slower than in the others, and its pitch dropping a little toward the end of the chirp. The male jerks his body backward at the end of this last chirp in each group of chirps.

A male encounter or fight chirp noted in this species (Plate XXXV) showed an increase in the number of pulses, a modification from the chirp of the calling song analogous to that occurring in Acheta and Miogryllus.

The calling and courtship songs of this species have been analyzed or described by the following authors:

Pierce (1948, 26, Franklin, New Hampshire) found a chirp rate of 1.4-5 per second with 4-12 (in one case 23) pulses per chirp. He obtained a dominant frequency of 7740 cycles per second at a pulse rate of 75 per second and a chirp rate of 1.3 per second.

Fulton (1931, 6 and 1932, 6) observed the following chirp rates: Ames, Iowa, 2.5-3/sec at 77° F., 4/sec at 80° F.; Raleigh, N. C., 3-5/sec at 86° F., 4-6/sec. at 88° F.; Ripley, W. Va., 3/sec at temperature probably over 90° F.; Geneva, N. Y., 3-5, "crickets in the sunlight and temperature well over 80° F. in the shade. At 66° F. a Raleigh male sang only 7 notes in 5 seconds."

Fulton noted further that introducing females into a cageful of males increased the chirp rate from 3, 4, and 5 per second at 86° F. to 4, 5, 7, and 8 per second, respectively. His comments on the courtship song are, "The mating song is similar to the above except that there is a brief pause after a series of 5-9 notes and the last note of each series is slightly prolonged with a decrescendo movement. This note is accompanied by a backward jerk of the body." The courtship songs observed in Ohio specimens had only 2-3 chirps per group.

Nemobius maculatus Blatchley

The Spotted Ground Cricket

Distribution

This species has been observed only a few times during this study, and was heard singing between August 19 and September 24. Fulton (1932, 6) records adults between mid-August and November 21 at Raleigh, N. C., and Blatchley (1920, 6) says it was quite frequent in Marion Co., Ind. on October 26. It is an inhabitant of leaf litter in dry forest, often occurring in company with *N. tinnulus* and the northern wood *Acheta*.

Singing Behavior

Only the calling song has been observed in this species. It sings both day and night.

Song Records

*Franklin Co., O. (Ohio State University Woodlot) 24 Sept 1954, 75° F., 2 min. 15 sec.

*Porter Co., Ind. (Dunes Park) 19 Aug 1954, 85° F., 1 min. 25 sec.

Hocking Co., O. (Ash Cave) 14 Sept 1954.

Song Description and Analysis

The calling song is a soft, high-pitched, continuous trill with a regular "skip" occurring at a rate of about 6 per second at 85° F. It is audible only a few yards away.

As shown in Plate XXXVI, the "skip" in the song is a slight gap after every 6th or 7th pulse, as if one pulse had been left out. The wingstroke rate for the pulses in each group of 6-7 is 45-50 per second. The dominant frequency in the song is around 6 kps., and each pulse is characterized by a sharp downslur. No courtship song has ever been heard, though males and females were caged together in the laboratory for some time.

The relationship of the calling song of this species to the pulsating trill of Nemobius carolinus (Plate XXXVI) is of interest, since that song has every 7th or 8th pulse de-emphasized, or softer than the others. This may illustrate one method of transition from continuous trilling songs to chirping songs in the evolution of rhythms of increasing complexity. If the break in the trill of N. maculatus were only a little longer, we would call this a chirping song rather than a trilling song. It would be worthwhile to know if the insect strokes its wings silently during this break, which is about the same length as one pulse plus an interval, or if it holds them motionless as do the chirping crickets, between groups of pulses.

This song has been described by Fulton (1931, 6, 1932, 6, Iowa and North Carolina) who called it a "... weak, continuous, buzzing trill with a constant rhythmical undulation in volume having a frequency about equal to the chirping rate of N. tinnulus....An Iowa specimen at 61° F. had 36 beats in 10 seconds; at 70° F. about 6 per second."

Nemobius palustris Blatchley

The Sphagnum Cricket

Distribution

This cricket has been observed on only 3 occasions during this study, at Cranberry Island on Buckeye Lake in Licking Co., O. This is a sphagnum-cranberry relict boreal bog and the only other Gryllinae on the island are N. carolinus and N. socius. The above observations were made between August 15 and September 15. Cantrall (1943, 6) gives the dates of July 12 and October 4 as the period between which adults are present in the bogs on the George Reserve, Michigan. According to Fulton (1951, 6), adults are present around Raleigh, North Carolina, from early August to November 1.

Singing Behavior

Only daytime observations were made on this species in the field, and it apparently sings considerably during the day.

Several specimens were caged in the laboratory for about ten days, along with specimens of N. socius and N. carolinus. The calling songs of these three species are not difficult to distinguish. Previously I had heard a sound from males of N. carolinus which was quite different from the calling song, and since it was produced around the females, I had presumed that it might be some sort of courtship song. A similar sound was heard and recorded from the cage containing all three of the above species. The room was dark when this recording was made, and this song was attributed to carolinus at the time. However, subsequent analysis of the song makes it appear that this song (Plate XXXVII) was probably produced by the palustris males and not carolinus. The pulse rate is about 40 per second at 85° F. which is near that of the calling song of palustris. The pulse rate in the calling song of carolinus at this temperature is about 75 per second. None of the "courtship" chirps heard from carolinus males was recorded.

The close relationship of these two species makes it likely that they might have similar courtship sounds. This chirp is different from the courtship sound of any other Nemobius, but is quite similar to the calling songs of N. confusus and apparently N.

sparsalus (Fulton, 1937, 6). It is not uncommon to find two closely related species in which one, usually apparently most like the "parent" species, has the courtship song like the calling song of the other (cf. *N. fasciatus* and *N. tinnulus*).

Song Records

*Licking Co., O. (Cranberry Island) 2 Sept 1954, 80° F. (1) 4 min. 10 sec., 40 pulses/sec., (2) 2 min. 10 sec., pulses/sec., (3) courtship, 4 min., 35 sec., 12 chirps.

Licking Co., O. (Cranberry Island) 15 Aug 1955, 15 Sept 1955.

Song Description and Analysis

The calling song is a thin, high-pitched trill, audible only a few yards away. The pulse rate at 85 F. is 35-40 per second, and the dominant frequency is around 6 kps.

This is not a continuous trill, and is not always uniform. In the 3 specimens recorded here, the trill length varied from 4 to 52 seconds, and the intervals between trill in sustained singing varied from a fraction of a second to 10 seconds in length. The trills start softly and build up in intensity, much like the chirp of *N. confusus*, and at the end of a trill, a short, detached group of pulses is often produced again much like those that often precede or follow the chirp of *N. confusus*.

This song is also very close to that of *N. carolinus*, and could perhaps best be described as somewhere intermediate between the alternately pulsating trill of that species, and the chirp of *N. confusus*.

A comparison of these three songs indicates one way that a chirping song may develop from a trilling song. The alternately pulsating song of *N. carolinus* is a rather unique, continuous trill. The calling song of *palustris* is like this song, containing both the rise in intensity and the short, pulsating portion (represented by the detached portion of the trill). However, the song of *palustris* is not continuous like that of *carolinus*, but is broken at irregular intervals. The calling song of *confusus* differs chiefly in that it is broken at *regular* intervals, and the trills have become much shortened. An additional relationship, already mentioned, is that both *carolinus* and *palustris* have courtship chirps which are nearly identical to the chirp in the calling song of *confusus*, though these are produced at wide intervals, and not regularly as are the chirps of *confusus*.

The calling song of *palustris* has been described by the following authors:

Allard (1911a, 6, Oxford, Mass.) "...a faint, quavering, high-pitched trill."

Walker (1904, 6, Ontario) "...a continuous and very feeble trill."

Morse (1920, 6, New England) "...a feeble, high-pitched, continuous trilling, sounding faint and far away even though the little creatures are at one's feet."

Cantrall (1943, 6, George Reserve, Michigan) "...a feeble, high-pitched, continuous trill, sounded both by day and by night." (under *cubensis palustris*)

Fulton (1932, 6, Raleigh, N. C.) "...Notes repeated continuously, for indefinite period.... Notes and rests about equal, usually 5 to 15 seconds, and weak, very high pitch; on ground; day and night ... on sphagnum moss."

Fulton (1931, 6, Geneva, N. Y. and Raleigh, N. C.) "...each note very gradually increases in volume until it ends abruptly. At Geneva, N. Y. on a hot day the notes of palustris were observed to be 5 to 10 seconds in length and the rests 5 to 10 seconds. At Raleigh, N. C. no difference in the song could be noticed. The species here has paler legs, head, and pronotum, and is close to if not identical with *N. palustris aurantius* Rehn and Hebard." Fulton later describes a similar song for *N. cubensis*.

Fulton's careful description of the calling song of this species differs from those given by all the other authors, who describe the trill as continuous. This could possibly be due to a lack of sustained observation by the other authors, although the possibility of geographic variation should not be ruled out. This is especially true in view of the morphological variation in this species, and its restriction to sphagnum bogs.

The calling songs of 2 of the 3 specimens recorded from Cranberry Bog at Buckeye Lake, Ohio, had trills and intervals (latter given in parentheses) with the following spacing (numbers represent seconds): 9 (1) 35 (1) 6 (1) 52 (1) 4 (1) 10/ / 45 (1) 6 (1) 15 (1) 35 (½) 14 (½) 50 (½) 9 (10) 12 (3) 19 (2) 20 (5)/.

The courtship chirps attributed to this species occurred at intervals (seconds) as follows: 25 - 12 - 8 - 5 - 39 - 53 - 28 - 9 - 34 - 26 - 32.

Nemobius carolinus Scudder

The Carolina Ground Cricket

Distribution

The Carolina ground cricket occurs all over the area studied, and its calling song can be heard from the latter part of June until freezing weather or very heavy frost at Columbus, Ohio. Like *N. fasciatus* and *N. socius*, this species is able to survive several frosts in the fall, due to the fact that it stays down in trash and leaf litter where the temperature remains somewhat higher later in the fall than in more exposed areas. These three species become surprisingly noticeable after the first frosts due to the disappearance of the louder species that "drown them out" earlier in the season.

It is difficult to describe the ecology of this species since it seems to occur almost everywhere. However, it is most abundant in damp areas, and is not found in high, dry, oak-hickory and oak forests. It is commonly encountered in swamp forest associations.

Singing Behavior

The calling song is produced both day and night. A presumed courtship chirp, already mentioned (p. 146-149), has been heard both in the field and in the laboratory.

Song Records

The calling song of this cricket has been heard at nearly every locality visited during the study, and was heard continuously from early July until October at Columbus, Ohio. Table 3 summarizes the recordings made of this species.

Table 3

Recordings of *Nemobius carolinus*

Date	Location	Temperature	Length of recording	Pulses per second	Frequency in cps.
1 July 54	Franklin Co. O.	90°F.	120	93	6000
24 July 54	Franklin Co. O.	62	38	74	5900
24 July 54	Franklin Co. O.	62	60	67	5500
24 July 54	Franklin Co. O.	62	42	64	5200
24 July 54	Franklin Co. O.	62	40	72	5500
24 July 54	Franklin Co. O.	62	42	62	4800
24 July 54	Franklin Co. O.	62	80	66	5400
24 July 54	Franklin Co. O.	62	35	66	5500
24 July 54	Franklin Co. O.	62	38	64	5500
28 July 54	Franklin Co. O.	74	70	76	6000
18 Aug 54	DePage Co. Ill	85	25	74	5800
21 Sept 54	Franklin Co. O.	65	25	66	6000
22 Sept 54	Franklin Co. O.	60	188	58	4100
22 Sept 54	Franklin Co. O.	60	70	57	4800
22 Sept 54	Franklin Co. O.	60	20	54	4600
22 Sept 54	Franklin Co. O.	60	50	56	4800
22 Sept 54	Franklin Co. O.	60	20	44	4500
23 Sept 54	Franklin Co. O.	50-55	90	43	4200
23 Sept 54	Franklin Co. O.	65	73	46	4200
25 Sept 54	Licking Co. O.	85	75	86	6200
25 Sept 54	Franklin Co. O.	—	78	58	4800
6 July 55	Franklin Co. O.	74	45	70	5750
6 July 55	Franklin Co. O.	71	28	68	5700
8 Aug 55	Raleigh, N.C.	79	—	90	6500
11 Aug 55	Bath Co. Va.	65	—	65	5000
15 Aug 55	Raleigh, N. C.	85	—	95	6200
5 Sept 55	Piatt Co. Ill.	58	—	59	4900
5 Sept 55	Piatt Co. Ill.	58	—	56	4600

Song Descriptions and Analysis

The calling song of this species seems to vary somewhat. The most commonly encountered song is a rapid, continuous, high-pitched trill which pulsates rapidly for a few seconds, then the pulsations disappear and the trill is smooth or even for a few seconds, then the pulsations reappear. This cycle is repeated over and over again. During the phase of steady trilling the speed of wing motion drops somewhat, in one specimen, for example, from a high of 93 strokes per second in the pulsating part to a low of 75 per second in the smooth part of the song. During the pulsating part of the trill, damped or softened pulses (the cause of the pulsating effect) occur every 7-12 pulses. As shown above, the pulse rate in this species varied from 43 to 95 per second between 50° F. and 95° F., and the frequency varies from 4.1 to 6.2 kps.

Several recordings attributed to N. carolinus are even, non-pulsating trills, and otherwise inseparable from the alternately pulsating trill; also, recordings have been made of continuously pulsating trills. On September 5, 1955, both types of songs were recorded from two specimens only ten feet apart in a clover stubble field in Piatt County, Illinois. The reason for these variations is not known. The only described species of Nemobius from this general area which has not been recorded (supposedly) is N. bruneri Hebard, concerning the song of which Fulton (1932, 6, p. 63) says, "Similar to last [N. fasciatus] but higher pitched, weaker, vibrato more rapid and not perceptible at high temperatures..." In correspondence, Dr. Fulton says that he too has noticed that N. carolinus specimens often sing a non-pulsating song.

A presumed courtship chirp, very similar to the calling songs of N. confusus, N. sparsalus, and to the courtship chirp of N. palustris, has already been mentioned (p. 146-149). It has not been recorded, but is a short trill lasting about one second, beginning softly and building up in intensity, then ending abruptly. It is given at wide and irregular intervals.

The calling song of this species has been analyzed or described by the following authors:

Walker (1904, 6, Ontario) "...a high-pitched, continuous trill of considerable volume."

Allard (1911b, 6, Washington, D. C.) "...a weak, low pitched, prolonged trill, almost indistinguishable from the trill of Nemobius palustris of New England except possibly a little louder."

Allard (1916, 6, Clarendon, Va.) Same.

Piers (1917, 6, Nova Scotia) "...a long, continuous, soft, rolling whirrrrrrr."

Morse (1920, 6, New England) "...continuous, high-pitched trill."

Cantrall (1943, 6, George Reserve, Michigan) has given a very careful description which corresponds closely to that given for the alternately pulsating trill described above. He says the complete cycles of pulsation versus non-pulsation occur at a rate of about 24 times a minute.

Fulton (1931, 6, North Carolina and Iowa) gives essentially the same description, addition, "Rarely males will be heard that seldom sing without beats, but usually there is a regular repetition of the two phases of the song, sometimes one second for each period and sometimes longer. Sometimes when starting to sing this species will sound a few notes which increase in volume and then die out."

With the exception of those given by Cantrall and Fulton, none of the above descriptions is complete enough to compare with those given here. Cantrall very clearly is describing the alternately pulsating trill, and Fulton has apparently noted all three of the variations discussed here. More investigation is needed to clear up the relationships of these three songs.

<u>Nemobius</u> <u>confusus</u> Blatchley

The Confused Ground Cricket

<u>Distribution</u>

This cricket apparently occurs all over the area studied. It is commonly encountered in damp forests, and also in pastures, stubble fields, along roadsides, and in lawns. I have most often heard it in damp forests where the singing male will often be found inside a dead, curled leaf. It is a difficult species to locate and capture because of its small size. At Columbus, Ohio, it sings from mid-July until heavy frost.

Hebard (1938, 6, Maryland) says this species is adult in mid-August and occurs in bogs and swamps.

Singing Behavior

This species sings day and night like the other Nemobius, and more individuals can usually be heard at any one time during the night than during the day. Few laboratory observations have been made, and no courtship song has been heard.

Song Records

*Porter Co., Ind. (Dunes Park) 19 Aug 1954 (temperature unknown, a warm, sunny day, probably 80-85° F.) 47 chirps in 63 sec.

*DuPage Co., Ill. (Bemis woods) 18 Aug 1954, 85° F., 58 chirps in 61 sec.

*Hocking Co., O. (Ash Cave) 11 Sept 1954, 65° F., 47 chirps in 1 min. 45 sec.

*Franklin Co., O. (Clinton Twp), (1) 28 Jul 54, 72° F., 31 chirps in 30 sec. (2) 24 July 54, 64° F., 18 chirps in 40 sec. (3) 30 chirps in 40 sec. (4) 90 chirps in 1 min. 45 sec.

Song Description and Analysis

The calling song is a regular succession of short trills (or long chirps), each lasting from ½-1 second and occurring at rates of 1 every 1 or 2 seconds. The sound is high-pitched (5-6 kps.) and rather soft. Each of the trills begins rather softly and increases gradually in intensity until it ends abruptly. Some individuals preface each trill with 1, 2, 3, or 4 short, soft pulsations, sometimes completely detached from the rest of the trill (Plate XXXVII). Sometimes little detached portions seem to come after the chirp rather then before it. If the intervals between the trills of this species were cut out, the result would be a song resembling very much the alternately pulsating trill of *N. carolinus*. In the song of specimen (4) above, there are places where two chirps are run together causing the song to sound very much like that of *carolinus*.

This song has apparently been described only by Fulton (1931, 6, Iowa and North Carolina). He observed specimens which attached 2 and 3 of the brief pulsations to the front of the trill. He gives trill (chirp) rates as follows: Iowa, 70° F., 1-2/sec; Raleigh, N. C., 75° F., 9-10/10 sec, and 80° F., 10-13/10 sec. He observed no courtship song in males caged with females.

The following is an analysis of one chirp from each of the recordings, based on Vibragrams.

Table 4

Analysis of Chirps of *Nemobius confusus*

Recording	Temperature	Frequency	Pulses/Sec.	Total Pulses/Chirp
1	80 F.	6.2 kps.	60	44
2	85	6.9	66	42
3	65	5.7	46	39
4	72	6.6	60	43
5	64	5.8	48	44
6	64	6.6	58	43
7	64	6.0	56	49

Gryllidae, Oecanthinae

The Tree Crickets

The calling songs of all the known species of tree crickets occurring in eastern United States have been recorded in this study. The number of species involved is doubtful, due to incomplete information concerning the Oecanthus nigricornis group, but it appears that there are at least nine and perhaps ten. These crickets all overwinter in the egg stage, and all but one species have only one generation per season; there are indications that O. argentinus Saussure has two generations per season in at least part of its range. O. argentinus is the first species to mature at Columbus, Ohio, having been heard singing on 29 June 1954. O. latipennis is the last to mature, beginning to sing about mid-August.

All of the tree- and bush-inhabiting species sing only at night; of those occurring most commonly on herbaceous vegetation all but one species, O. latipennis, sing both day and night.

Apparently all of the male Oecanthinae possess a metanotal gland (Hancock's Gland) which attracts the female (Fulton, 1915, 6). No well-defined courtship song is known in any of the species. The tegmina are held at approximately a 90° angle, both during the calling song and the courtship display, and during the erratic singing that occurs during courtship. The female mounts the male under his lifted tegmina.

The males are sedentary, though they often occur in great density in the species found on herbaceous vegetation. Their songs are relatively loud, clear, musical trills (most species) or chirps (one species), pitched between 2 and 4 kilocycles per second.

Only one species in this group (Oecanthus niveus) has a chirping song, "susceptible" to the development of synchronization or alteration, and in this species synchronization is well-developed.

Oecanthus angustipennis Fitch and O. exclamationis Davis

The Narrow-Winged Tree Cricket and Davis' Tree Cricket

Introduction

No way has yet been found to distinguish the calling songs of these two tree crickets. They occur in similar habitats, often together, and they are both arboreal, exclamationis perhaps more strictly so than angustipennis. As a result my observations on these two species have been rather scanty, and in most cases I have been unable to say which of the two species was involved. Only 3 positively identified recordings have been made, 2 for angustipennis and 1 for exclamationis. These were used to make the Vibragrams in Plate XXXVIII. Whether or not the differences between the songs of these individuals occur consistently between the two species, I cannot say. Plate XXXIX compares all the recordings made of these two species and Neoxabea bipunctata with respect to pulse rate and frequency at similar temperatures.

O. angustipennis was collected on cocklebur, blackberry (nymphs, July 27, Cedar Point, O.), and plum (singing male, 19 Aug). O. exclamationis was collected on elm and hackberry between late

PLATE XXXVIII. CALLING SONGS OF TREE CRICKETS

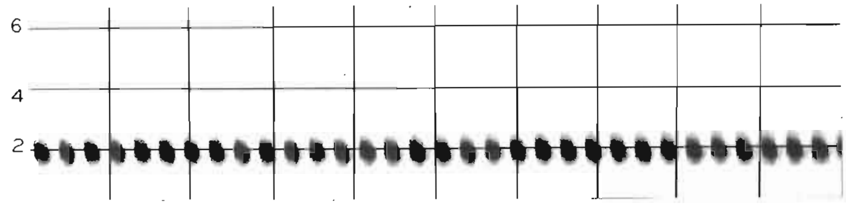


Fig. 98. OECANTHUS LATIPENNIS 65°F.

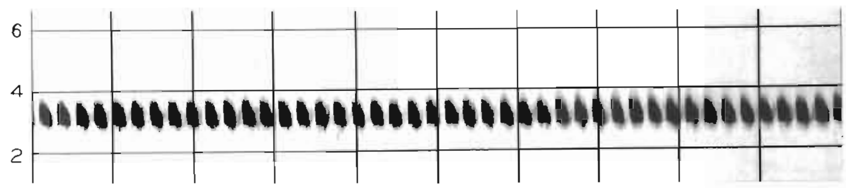


Fig. 99. OECANTHUS PINI 78°F.

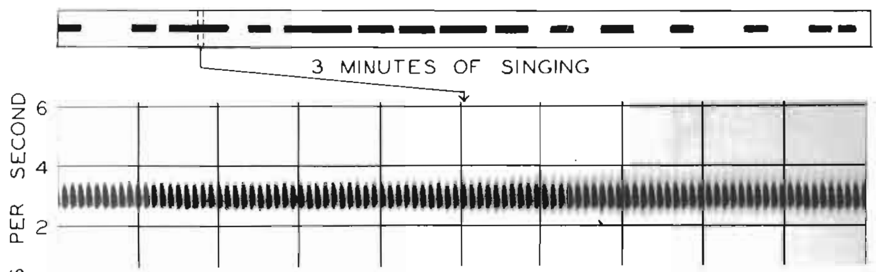


Fig. 100. NEOXABEA BIPUNCTATA 74°F.

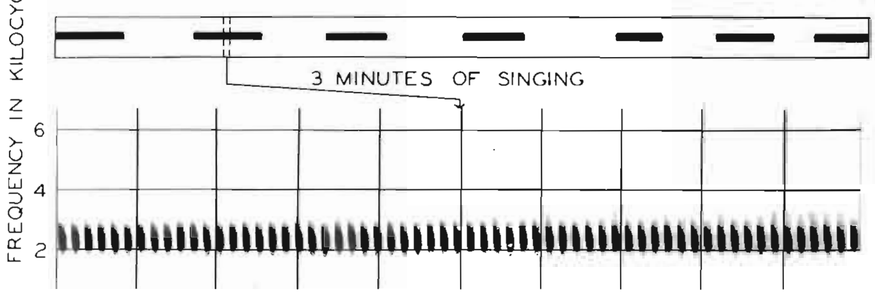


Fig. 101. OECANTHUS ANGUSTIPENNIS 71°F.

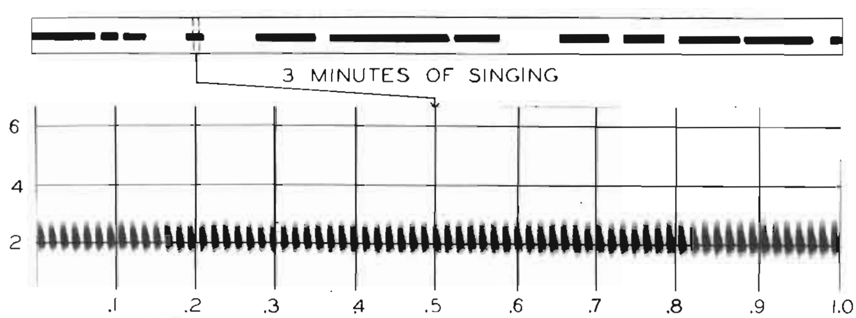


Fig. 102. OECANTHUS EXCLAMATIONIS 71°F.

TIME IN SECONDS

PLATE XXXIX. PULSE RATE AND FREQUENCY IN THE SONGS OF _OECANTHUS ANGUSTIPENNIS_, _O. EXCLAMATIONIS_, AND _NEOXABEA BIPUNCTATA_

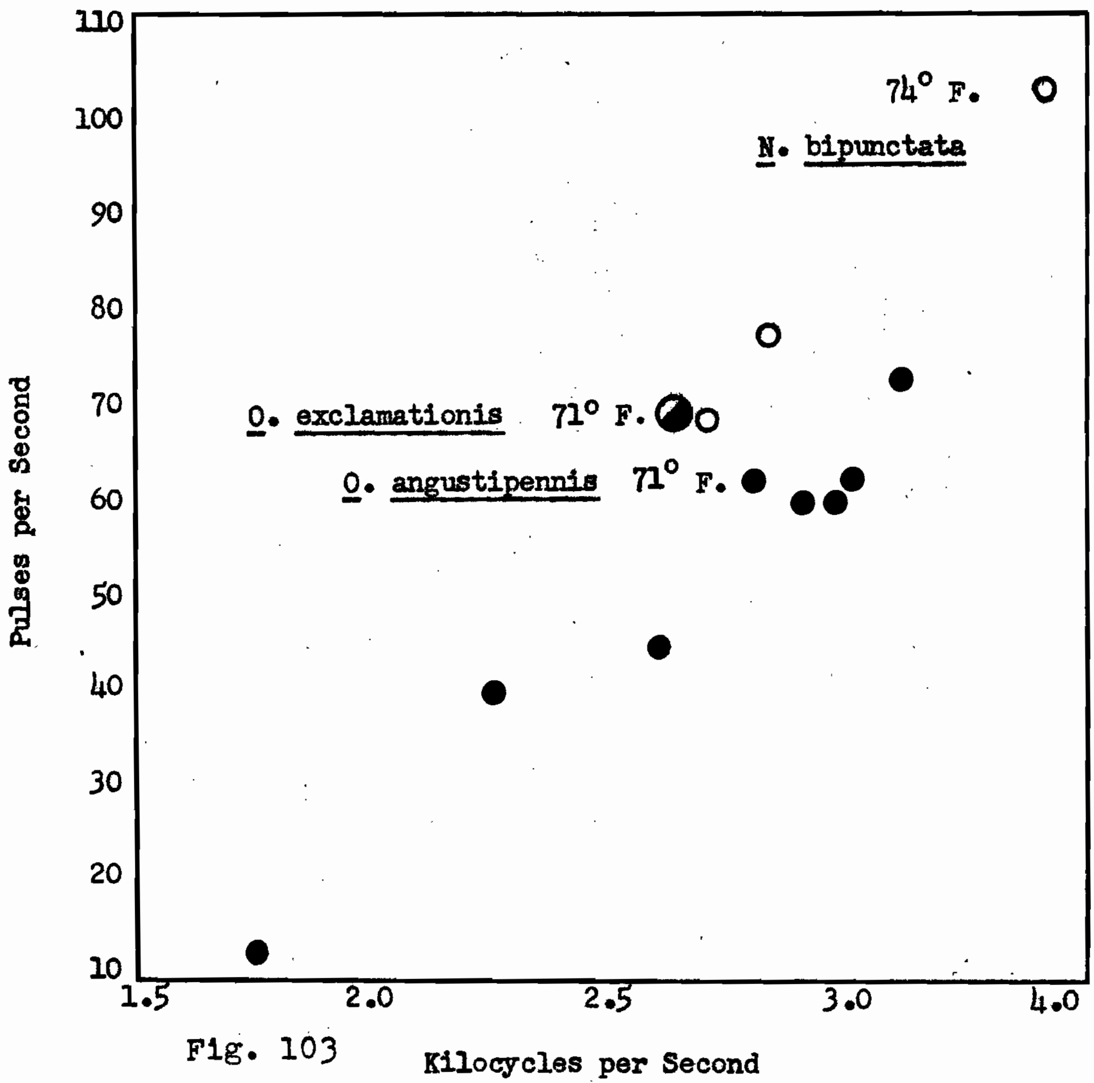


Fig. 103

July and Late September (adults). Hebard (1938, 6, Pennsylvania) says exclamationis is "more definitely arboreal than any of the other species of the genus. Prefers oaks, maples, and other deciduous trees...Appears adult in late July." Of angustipennis he says "...Prefers shrubbery and is often present locally in very large colonies. Appears adult in mid-August, greatest abundance in late fall." Fox (1917, 6, Charlottesville, Va.) found angustipennis "on oak in open grove" July 14-17. Cantrall (1943, 6, George Reserve, Michigan) says of angustipennis "...characteristic of the deciduous-arboreal stratum of the Reserve. It has been seen and heard on American elm, white oak, black oak, sassafras, sugar maple, and white ash. In the upland woods, the species also occurs characteristically in the tall shrub stratum, but it is not present in the low shrub-terrestrial stratum." Later he says, "Owing to its strictly arboreal habits I was able to secure only two adults." He obtained these specimens on August 17, 25, and July 18. On the basis of song records he states that males were still common on September 21. Neither Cantrall nor Fox mention exclamationis.

Blatchley (1920, 6) says angustipennis "frequents the borders of groves and especially ironweeds in open pastures and reaches maturity about July 15," in Vigo, Putnam, Lawrence, Floyd, and Crawford Counties, Indiana. In Florida he says he has taken adults of angustipennis by beating and sweeping in October, December, January, and March, "and it has been sent in as taken at porch light in May and June."

Fulton (1951, 6, North Carolina) says, "This species and the following (exclamationis and angustipennis) have songs so similar that they cannot be distinguished with certainty. Both live mainly in the tops of forest trees so that it is difficult to obtain specimens. Probably the song periods overlap. There is no time in August when none can be heard but during some years there has been a noticeable drop in the number singing about the middle of the month." He gives the song periods of the two species as from late June to mid-August for exclamationis, and mid-August to November 8 for angustipennis. Of angustipennis he says, "...The earliest adult captured was a recently matured one on July 21, 1930. This is an unusual record in view of the fact that on August 13, 1934, several nymphs were collected but only one adult and on August 25, 1934, some nymphs could still be found." Of the ecology of these two species he says in 1932, for exclamationis, "Usually in oaks," and for angustipennis, "Various trees, sometimes found on herbs and bushes under trees."

Strohecker (1937, 26) found angustipennis in northern Illinois on black oak on sand, oak-hickory on clay, and in a climax sugar maple forest at Joliet, Illinois, and a damp forest at Smith, Indiana.

Friauf (1953, 26) lists angustipennis as an occasional (20-50% frequency) abundant in the "scrub stratum" of the "scrub habitat" on the Welaka area in northern Florida.

Singing Behavior

Both of these species sing chiefly at night, although on several occasions individuals were heard singing during the day, often at noon on sunny days, but deep in heavy, vine-filled swamp forest where the light intensity was relatively low. Cantrall (1943, 6) records similar observations: "...they [angustipennis] are usually heard only at night or on cloudy days. Males, however, were twice heard singing in perfectly clear weather, about 2 P. M., during the hottest part of the day." Allard (1910b, 6, North Georgia) says of angustipennis, "It sings on cloudy afternoons, though its song is best heard after sunset."

I have never found singing males of either angustipennis or exclamationis perched less than 6-7 feet above the ground, and only on two occasions, one for each species, have I found them less than 10 feet above the ground. The song attributed to one or the other or both of these species is characteristic of wooded areas throughout the area studied, always coming from the forest canopy, usually more than 20 feet from the ground. In most cases so many individuals sing that the sound is continuous from dusk until sometime early in the morning, though the song of any one individual is discontinuous, made up of bursts of song and breaks of similar length.

As is often the case with the tree crickets, the two males of these species observed singing were clinging to the underside of leaves, with their antennae, head, pronotum, and front legs extending across the edge of the leaf, as shown in Plate I. There seems to be no alternation or synchronization of songs, though acoustic stimulation probably occurs. Neither species was observed in the laboratory, so nothing is known of the courtship behavior.

Song Records

*Carroll Co., O. (Berghola) 14 Aug 1954, 66° F., 65 sec. (song identified as *O. angustipennis* by Dr. E. S. Thomas).

*Franklin Co., O. (Clinton Twp.) 23 Aug 54, 71° F., 75 sec. (*angustipennis*, specimen captured).

*Franklin Co., O. (Borror) 1 Sept 54 (no temperature given) 2 min. (*angustipennis*, specimen captured).

*Franklin Co., O. (Borror, no temperature given) (1) 15 Sept 54, 2 min. 23 sec. (2) 18 Sept 54, 1 min. 3 sec., (3) 23 Aug 54, 1 min. 56 sec., (4) 1 Oct 54, 2 min. (none identified).

*Piatt Co., Ill., 4 Sept 55, 65° F. (not identified).

*Franklin Co., O. (Clinton Twp) 28 July 54, 70° F., 30 sec. (*exclamationis*, specimen captured).

Song Description and Analysis

The song is a rather continuous succession of clear, low-pitched trills of varying lengths, and separated by equally variable intervals (Plate XXXVIII). In Plate XXXIX, pulse rate is plotted against frequency for samples from these nine recordings and the three recordings made in this study of *N. bipunctata*. The positively identified recordings are designated, and the known temperatures are indicated. The single specimen of *exclamationis* seems to have a somewhat higher pulse rate at the same temperature and frequency than all the other recordings of either *angustipennis* or *exclamationis* which fall in a fairly uniform pattern. Perhaps further recording of *exclamationis* will show that there is only one recording of *exclamationis* involved here, and that a consistent difference exists between the two species in this respect.

The following table gives the lengths of trills and trill intervals for the calling songs of six individuals of these two species, and for the three recorded specimens of *N. bipunctata*.

Table 5

Song Analysis for *Oecanthus angustipennis*,

O. exclamationis, and *Neoxabea bipunctata*

Species	Length of Trills			Length of Intervals		
	No.	Range	Mean	No.	Range	Mean
O. exclamationis	8	1.0 - 6.3	3.4	7	.25 -4.25	.9
O. angustipennis	16	1.25-4.75	2.68	14	1.0 -9.25	3.75
Unidentified Recordings	17	.25-43.75	4.25	7	.5 -2.25	1.5
	13	1.0 -2.75	3.25	12	1.25-5.6	3.0
	37	.5-4.0	1.81	35	.5- 4.5	1.975
	47	.5-3.0	1.525	46	.5- 4.0	0.935
N. bipunctata	33	.75-2.5	1.44	31	.25-3.0	1.825
	5	1.75-9.25	5.6	4	.063-.375	0.235
	3	2.5 -6.0	3.8	2	2.75 -4.75	3.75

These figures indicate that there is little or no difference among the three species in the length and spacing of trills.

The songs of *angustipennis* and *exclamationis* have been described by the following authors:

Fulton (1915, 6, New York, *angustipennis*) Pitched "from C# to D#, 2 octaves above middle C, depending on temperature and somewhat on individual variation. Each trill continues from one to five seconds, but most commonly it lasts for about two seconds. The periods of rest vary more and may be from one to eight seconds or longer." (generally not over 10 trills per minute, but up to 15). One caged individual sang continuously for over a minute.

Fulton (1915, 6, New York, exclamationis) "...intermittent and non-rhythmical and most resembles the song of angustipennis. The pitch is the lowest of any species studied (all except N. bipunctata and O. californicus), and reaches only to the second B above middle C. The common length of note and rest is two or three seconds, but this varies much as in the song of angustipennis. The beginning of each note is comparatively weak, but the sound increases in volume and slightly in pitch and continues uniformly until it abruptly ends.

Snodgrass (1923, Washington, D. C., angustipennis) "...a soft burr-r-r, prolonged about two seconds, and repeated at intervals of equal length."

Allard (1910b, 6, Thompson's Mills, Georgia, and New England, angustipennis). "In New England, a faint, brief high-pitched pre-e-e.. does not sustain the same uniform pitch, but dies away in a slightly lower key...prefers low shrubs, best of all the tangles of vines and sweet fern bowers in the pastures...seem to sing in louder, more vehement tones than those..in North Georgia where it appears more strictly arboreal than any other cricket...amidst the foliage of tall oak trees."

Cantrall (1943, 6, George Reserve, Michigan, angustipennis). Trills last 1-6 seconds, intervals 1 to many seconds, and occasionally minutes. One male sang 17 trills in 45 seconds.

Fulton (1932, 6, North Carolina, angustipennis). Notes over one second long, seldom over 10 seconds, longer than rests except when starting to sing. Does not distinguish from exclamationis.

Beutenmuller (1894, 6, New York). Trills lasting about 5 seconds, equal intervals.

The slight rise in pitch or frequency at the beginning of each trill, mentioned by Fulton (1915, 6) has been noticed repeatedly in this study. It seems to occur almost inevitably, and is associated with a slight rise in rate of pulsation.

The only disagreement in the above descriptions with the analysis given here is Fulton's indication that exclamationis has a lower pitched song than angustipennis. The single specimen recorded here had a substantially higher-pitched song than the 2 specimens positively identified as angustipennis.

Neoxabea bipunctata (DeGeer)

The Two-Spotted Tree Cricket

Distribution

This species apparently occurs all over the area studied, and has been heard from mid-July until late September at Columbus, Ohio. It is an arboreal species, and has been collected from hackberry, elm, sassafras, and apple. On only two occasions has it been found singing within reach of the ground; it usually sings from 10 feet or higher in trees.

Fulton (1932, 6, Raleigh, North Carolina) says this species is found in vines, bushes, and trees. Hebard (1938, 6, Pennsylvania) says it "prefers vine tangles in openings of woodlands and along forest borders. Appears adult in early August."

Singing Behavior

This cricket is a night-singer. It begins rather uncertainly in the evening, with trills that are much shorter than those occurring later in the night when it is in "full song." A given individual may sing in short spells several times in the evening before beginning continuous song. Sometimes the trills given at such times begin with a pulse rate apparently about half the usual rate, then jump to the usual rate before their end.

No observations have been carried out on the courtship or copulation of this species, and only the calling song is known.

Song Records

*Franklin Co., O. (University Woodlot) 28 July 1954, 74° F., 2 min. 22 sec.

*Williams Co., O. (Northwest Twp.) 19 Aug 1954 (1) 32 sec., (2) 24 sec. (Temperature unknown).

Franklin Co., O. Heard in Clinton and Blendon Townships throughout August and September, 1954 and 1955.

Song Description and Analysis

This song is a more or less continuous succession of rapid trills lasting from less than one second to a minute or more and separated by intervals almost as variable in length. Sometimes the intervals are quite short, only a fraction of second in length, giving a "stuttering" effect. The spacing of trills in the recordings made of this species is shown in Table 5. The song is of essentially the same structure and very similar to the songs of O. angustipennis and O. exclamationis, but is higher-pitched and has a more rapid pulse rate (Plates XXXVIII, and XXXIX).

The song of this species has been described by the following authors:

Allard (1910b, 6) Thompson's Mills, Georgia
Morse (1920, 6) New England
Fulton (1932, 6) North Carolina

Fulton says on warm nights the trills may last 15-30 seconds with very brief rests, and when starting to sing before dark the trills are 2-10 seconds long with ½-1 second rests.

One of the factors making it difficult to accurately compare the song of this species and those of O. angustipennis and O. exclamationis is that disturbed specimens, at least in the first two species mentioned, often shorten the length of the trills in their songs and lengthen the intervals between trills.

The songs of these three species are more variable in the characters which are readily discernible to the human ear than are those of any other species studied. They are perhaps closer to the primitive condition in this respect than any other type of rhythm, with both continuously trilling and chirping songs having probably developed from such irregular or variable patterns.

The <u>Oecanthus nigricornis</u> Group

<u>Introduction</u>

The taxonomic status of the three forms at present recognized in this group has continued to remain uncertain, despite the accumulation of a great deal of information on their morphological, ecological, distributional, and seasonal relationships over a large part of the United States. Most of our information is due to the excellent study by Fulton (1927, 26). The new information added here is with respect to song and seasonal relationships, the discovery of a possible fourth form in southeastern United States, and a confirmation of the distinctness of the three forms that occur in Ohio. Fulton's summary (P. 61) is quoted in part below.

> Three tree crickets of the genus <u>Oecanthus</u>, namely <u>nigricornis</u>, <u>quadripunctatus</u>, and <u>argentinus</u>, differ from each other mainly in color characters and have been separated by the nature of the black markings on the two proximal antennal segments. There has been some dispute among taxonomists as to whether they represent distinct species.
>
> In the eastern portion of the United States corresponding roughly to the country originally largely covered with forest, <u>nigricornis</u> and <u>quadripunctatus</u> are present and distinct in color characters, ecological distribution and habits, as well as having distinct types of eggs. They could be considered as separate species if they did not

extend beyond this region.

In the Great Plains region, nigricornis, quadripunctatus and argentinus are found, with many intermediate forms. The three are often associated in the same field on the same kinds of plants. The characteristics which typify nigricornis gradually disappear from the population toward the west, while the reverse is true of argentinus characters, which come no farther east than the true prairie regions.

Only argentinus and quadripunctatus are found in the Rocky Mountain region and are not clearly separated. The former only has been found in the Pacific Coast region.

Quadripunctatus has the same distinct type of egg in N. Y., Ohio, Fla., and Iowa. In the western region the eggs of individuals falling in the quadripunctatus classes of antennal patterns are of a different type and resemble those of typical argentinus.

Until better characters are discovered for separating the three tree crickets of this group, it seems advisable to consider them as subspecies.

Numerous other authors have expressed opinions on this group. Among these are Walker (1904, 6 Ontario), Houghton (1909, 26, Delaware) who also quotes Caudell, and Blatchley (1920, 6, Indiana), all of whom believed the three classical morphological forms to be "color varieties." Houghton reared crickets from several rows of eggs found together on common alder, and obtained nymphs which Caudell identified as quadripunctatus and two adults (one male and one female) which Caudell identified as "typical nigricornis." Later Houghton says he found all three forms (nigricornis, argentinus, and quadripunctatus) together in the field, and that he got a male of argentinus to mate with a female of quadripunctatus in the laboratory. Houghton's work was done in Delaware, and his mention of argentinus is puzzling since other workers (e.g., Fulton, 1927, 26) have stated that this form did not extend nearly this far eastward. In Ohio argentinus seems to stop somewhere near central Ohio. Houghton's material was identified by Caudell, whose concept of argentinus was apparently different from that of Fulton and other later workers.

Allard (1911a, 6, Fort Hill, Massachusetts) was unable to find any constant differences which serve to distinguish the songs of nigricornis and quadripunctatus. Later he says, "The stridulations of O. quadripunctatus in New England have always seemed louder and and lower-toned to the writer than the weaker and shriller trilling of the same species in northern Georgia." Allard apparently had very keen ears and this was a shrewd observation, since, as shown in Plate XL, and discussed below, a southern form with the markings of quadripunctatus and the shriller, more rapid trill of nigricornis or argentinus does occur. Cantrall (1943, 6, Michigan), like Allard, was unable to distinguish the songs of nigricornis and quadripunctatus, though he states that nigricornis matures in mid-August and quadripunctatus in late July or early August, and while nigricornis "...generally associated with dogwoods and shrubby Salix in the wet-shrub zone habitat...," nigricornis was "...a characteristic and common species of the mixed grass-herbaceous habitat."

Faxon (1901, 6, Cambridge, Massachusetts) states that the song of quadripunctatus is "...clearer in tone and no doubt sufficiently distinct on close acquaintance" (from that of nigricornis).

PLATE XL. OECANTHUS NIGRICORNIS GROUP

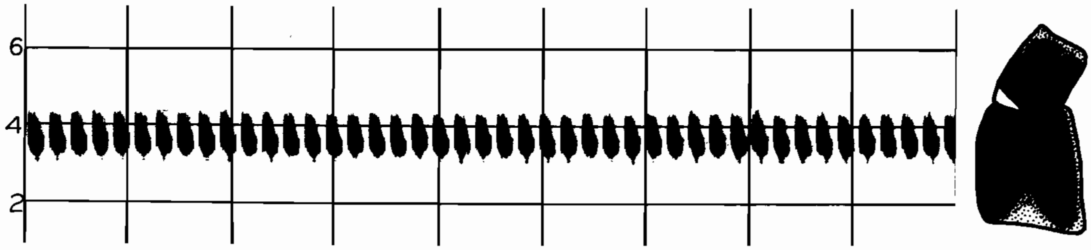


Fig. 104. NIGRICORNIS

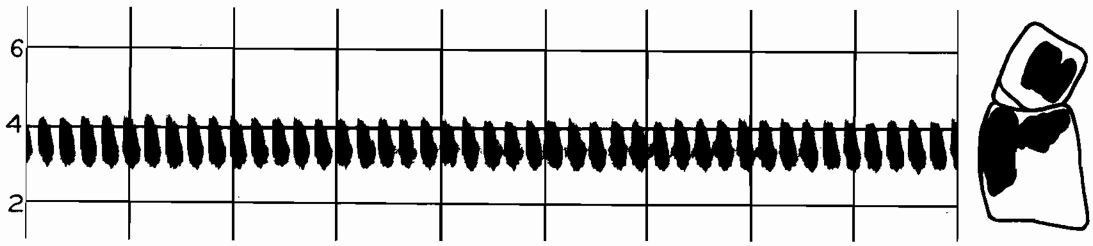


Fig. 105. ARGENTINUS

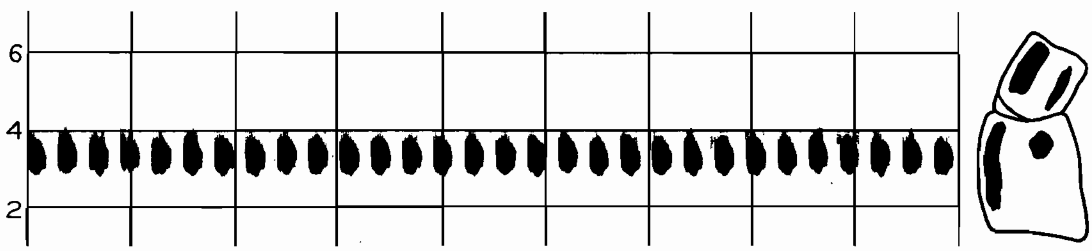


Fig. 106. NORTHERN QUADRIPUNCTATUS

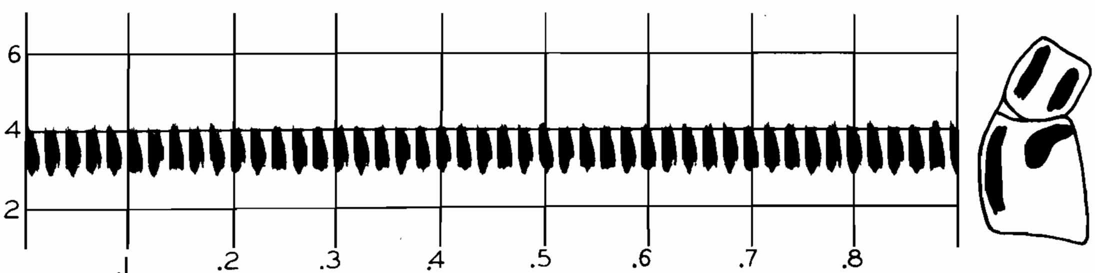


Fig. 107. SOUTHERN QUADRIPUNCTATUS

FREQUENCY IN KILOCYCLES PER SECOND

TIME IN SECONDS

Three or four populations have been encountered in this study, including three morphological forms and at least two song forms. Differences in ecology, distribution, and seasonal relationships are apparent between populations distinguishable by one method or another.

In Ohio, Indiana, and Illinois, the three morphological forms (*nigricornis*, *quadripunctatus*, and *argentinus*) are present, with some differences in ecology, and possessing among them two fairly distinct songs. *Nigricornis* and *quadripunctatus* seem to have but one generation per season, while *argentinus* apparently has two generations except in the easternmost portion of its range in central Ohio.

In southeastern United States, below the Appalachian Mountains, only one of the morphological forms (*quadripunctatus*) is present, but the song heard in North Carolina and Virginia in August was like that of the northern forms *nigricornis* and *argentinus*, and as with the northern *argentinus* there are apparently two generations per season in North Carolina (Fulton, 1951, 6). In Ohio, Indiana, and Illinois, the trill of *quadripunctatus* is slower and lower-pitched than the trills of *nigricornis* and *argentinus*.

Oecanthus argentinus Saussure

Distribution

The cricket bearing the markings generally assigned to this form appears in central Ohio before either of the other two forms that occur there. With the exception of Miogryllus verticalis, it is the first egg-overwintering orthopteran to mature in this area, beginning to sing in early June and ceasing sometime in late July at Columbus, Ohio. In Piatt County, Illinois, crickets with the same antennal markings and same song were found in great abundance in an alfalfa field on September 5, 1955, both as adults and late instar nymphs. Yet near Columbus, Ohio, fields containing large numbers of this species during June and July had only nigricornis and quadripunctatus during August and September. It seems likely that this species has two generations in the western part of the area studied, but only one from some point west of Columbus, Ohio, eastward. Its eastern limits are not known, but Columbus is apparently a new record and it is probable that it does not extend far beyond here. It was not encountered on collecting trips to Licking and Carroll Counties in 1954 and 1955.

Argentinus is generally found on coarse weeds such as giant ragweed (Ambrosia trifida), Queen Anne's lace (Daucus carota), sweet clover (Melilotus spp.), goldenrod (Solidago spp.), lamb's quarter (Chenopodium album), alfalfa, and corn. Like nigricornis, it is usually 3 or 4 feet above the ground, but is also frequently found nearer the ground, on such plants as alfalfa.

Singing Behavior

The calling song is produced both day and night, perhaps more at night. During courtship the wings are vibrated irregularly, sometimes producing sound and sometimes silently.

Song Records

*Adams Co., O. (Jefferson Twp.) 9 July 1954 (1) approximately 80° F., 1 min. 58 sec., (2) 85° F.

*Franklin Co., O. (Clinton Twp.) 8 July 1955 (temperature not recorded) (1) 1 min. 20 sec., (2) 35 sec., (3) 1 min. 40 sec. (courtship).

*Franklin Co., O. (Clinton Twp.) 29 June 1954 (temperature about 75° F.) 1 min. 23 sec.

Song Description and Analysis

The calling song is a continuous, clear trill, like a high-pitched police whistle being blown continuously. It is somewhat more rapid and a little higher-pitched than the quadripunctatus encountered in Ohio, with a pulse rate of about 50 per second and a frequency of 3.6 kps. (85° F.).

Courtship was observed both in the field and in the laboratory. The male keeps his tegmina elevated to about a 90° angle all the time that the female is near, and continually faces about and backs toward her. A large part of the time the tegmina are held still, but occasionally, especially if the female backs away from the male or otherwise avoids him, they are vibrated irregularly, producing short trills. Sometimes they are vibrated silently, with the file and scraper apparently not engaged. The female mounts the male under the lifted tegmina and feeds at the secretions of the metanotal gland. Actual transference of the spermatophore was not observed.

Oecanthus nigricornis Walker

The Black-Horned Tree Cricket

Distribution

The black-horned tree cricket occurs all over the area studied, but extends only to the southern border of the Appalachians in North Carolina. It matures in late July at Columbus, where its song can be heard until the first heavy frosts, and apparently has but one generation per season. I have found it on giant ragweed, blackberry, sweet clover, hogweed, cockleburr, and many other coarse weeds and bushes. It probably occurs in greater numbers on giant ragweed than all other plants combined where this plant is available.

Hubbell (1922, 6, Michigan) found adults between August 31 and September 6, usually with *quadripunctatus*. On one occasion he found *nigricornis* alone in a rank growth of tall herbaceous plants, vines, and shrubbery in a lowland thicket. He also says that *nigricornis* was more common than *quadripunctatus* in roadsides and forest margin thickets.

In Ohio, Indiana, and Illinois, *nigricornis*, *quadripunctatus*, and *argentinus* have been found together on the same plants, and two of these forms have been found together this way even more frequently. Neither of these cases are the most commonly encountered situation, However, and more often only one of these forms is found in a certain area, or on a certain plant at a certain height. If a continuously trilling tree cricket is singing from 3-4 feet or more above the ground in coarse weeds, it is almost certain to be *nigricornis* or *argentinus* (or *latipennis*). If a similar song is heard within two feet of the ground on fine-stemmed plants or grasses, it is almost invariably *quadripunctatus*.

Singing Behavior

The calling song is produced both day and night. Courtship has not been observed.

Song Records

*Franklin Co., O. (Clinton Twp.) (1) 21 Sept 54, 65° F., 33 sec. (2) 28 July 1954, 74° F., 54 sec. (3) 28 July 1954, 70° F., 35 sec.

*Erie Co., O. (Cedar Point) 26 July 1955, 78° F., 35 sec.

*DuPage Co., Ill. (1) 16 Sept 55, 72° F., (2) 9 Sept 55, 78° F.

Piatt Co., Ill. (Sangamon Twp.) 4 Sept 55, 88° F. (1) 30 sec. (2) 18 sec. (3) 24 sec.

Song Description and Analysis

This song is a continuous trill, a little less clear and a little higher-pitched and more rapid than the others in this group — definitely more so than northern *quadripunctatus*. It has a pulse rate of about 50 per second (Plate XIII), and is pitched at 3.6-3.8 kps. (74° F.).

Oecanthus quadripunctatus Beutenmuller

The Four-Spotted Tree Cricket

Distribution

The four-spotted tree cricket occurs all over the area studied, though the southern specimens, as shown in Plate XL, have a song like the northern *argentinus* and *nigricornis* and two generations a season; in the specimen used for the comparison in this figure (Coll. by Thomas Walker in Dyar Co., Tenn.), the antennal markings have a slightly different conformation than in the *quadripunctatus* found in Ohio, Indiana, and Illinois. The remaining remarks will apply only to the northern *quadripunctatus*. The southern form may represent a fourth population, or a clinal variation in one of the northern forms. The information at hand is insufficient to do other than point out that some sort of variation does exist, and that further study is needed for clarification.

At Columbus, Ohio, *quadripunctatus* matures in late July and sings until frost. It occurs most often near the ground on fine-stemmed plants and grasses, such as timothy, bluegrass, ragweed, dandelion, pasture daisy, and buckhorn. Singing males are often found only a few inches above the ground.

Hubbell (1922b, 6, North Dakota) found adults between July 28 and August 31 in grassy fields, roadside vegetation, patches of tall herbage, and in the brushy margins of woods. His description of antennal markings indicates that he had both *argentinus* and quadripunctatus, though he states, "They undoubtedly belong to the same species."

Hubbell (1922b, 6, Michigan) found adults from August 30 to September 9 among tall herbaceous growths, roadside and forest margin thickets, fields of second-growth scrub sedge and lizard's tail marshes, in dry, grassy fields, especially in ragweed, and in grass and grapevines alongside a dune blowout.

Singing Behavior

The calling song is produced both day and night. Courtship has not been observed.

Song Records

*Franklin Co., O. (Clinton Twp.) (1) 3 Aug 1954, 69° F., 30 sec., (2) 5 Aug 1954, 66° F., 28 sec. (3) 28 July 1954, 74° F., 40 sec., (4) 28 July 1954, 72° F., 58 sec.

*Erie Co., O. (west of Berea) 26 July 1955, (1) 76° F., 18 sec. (2) 23 sec.

*DuPage Co., Ill. (1) 9 Sept 1955, 78° F., 18 sec. (2) 16 Sept 55, 72° F., 28 sec. (3) 22 sec.

*Dyar Co., Tenn. (recorded by Thomas Walker) 23 Sept 55, 70° F., 60 sec.

Song Description and Analysis

As shown in Plate XL, the song of the northern form is a clear, continuous trill with a pulse rate of about 33 per second, and a frequency of about 3.5 kps. (72° F.). On the other hand, the specimen recorded in Dyar Co., Tenn. by Thomas Walker, Jr., which seemed to have a song identical to specimens heard in North Carolina and Virginia in August, 1955, has a pulse rate of 50 per second at 78° F., which is much nearer the pulse rate of argentinus and nigricornis.

Oecanthus pini Beutenmuller

The Pine Tree Cricket

Distribution

This cricket has been observed during this study on only one occasion in Ohio (Hocking Co., 3 Sept 1954, on Pinus virginiana), and otherwise only in August in North Carolina and Virginia. Fulton (1932, 6) records adults between early July and early September in North Carolina. Hebard (1938, 26, Pennsylvania) states that it is arboreal, inhabiting only pine trees in dry, sandy areas (pitch pine and scrub pine, Pinus rigida and Pinus virginiana), and that adults appear in late July. Cantrall (1943, 6, George Reserve, Michigan) records it from tamarack and indicates that the adults are probably present between late July and late September.

Singing Behavior

This cricket is one of the most difficult to locate and capture. I have never found it less than 6 or 7 feet above the ground, and it is usually much higher than this. Individuals often rest with their head directed toward the twig upon which they are located and the abdomen and tegmina parallel with the pine needles. Since the head and thorax are reddish-brown and the tegmina and abdomen a dark green, surprisingly near the color of pine needles, the insect is very difficult to spot in this position.

Only the calling song has been observed in this species.

Song Records

*Hocking Co., O. (Neotoma) 3 Sept 1954, 65° F., 55 sec.

*Raleigh, N. C., 8 Aug 1955, 78 F. (Thomas Walker)

*Bath Co., Va. (Warm Springs Mt.) 10 Aug 1955, 63° F., 32 sec.

Lenoir, N. C., 7 Aug 1954

Song Description and Analysis

This song is a clear, continuous trill, inseparable by ear from that of O. quadripunctatus except that it comes from pine trees and at night only. At 78° F. it is pitched at about 3.2-3.4 kilocycles per second and has a pulse rate of about 45 per second (Plate XXXVIII).

Fulton (1915, 6, N. Y.) says the song of this species if on the average about a note and a half lower in pitch than the songs of nigricornis and quadripunctatus, or the third E above middle C.

Cantrall (1943, 6, George Reserve, Michigan) could separate the song from those of nigricornis and quadripunctatus only by its lower pitch.

Pierce (1948, 26, Franklin, N. H.) gave a pulse rate of from 19 to 55 per second, and two frequencies, 1815 cps. and 3166 cps., of which he says, "This 1815 is a teeth-impact frequency, whereas the other frequency, 3166, cannot be a teeth-impact frequency without using all the teeth. It is probably wing-resonance frequency." Pierce found 47 teeth in a file 1.67 mm. in length.

Oecanthus latipennis Riley

The Broad-Winged Tree Cricket

Distribution

This cricket apparently has its northern limits somewhere in the central parts of Illinois, Indiana, and Illinois. At Columbus, Ohio, it is the last tree cricket to mature, beginning to sing in middle or late August. A large percentage of the population is probably killed by frost. At the Ohio State University woodlot this cricket is common along the border of the woods, in weedy ditches, and in grassy and weedy clearings.

Fox (1917, 6, Virginia) records this species from old stubble fields, roadside thickets, and dry, open woods of mountain summit, adult between August 21 and November 12. He found nymphs on August 12.

Blatchley (1920, 6, Indiana) says this cricket occurs throughout the southern part of that state on shrubs and vines along fencerows, roadsides, and especially in thickets along the borders of streams, with adults having been taken the last of August, and most abundant in October.

Hebard (1938, 6, Pennsylvania) says the broad-winged tree cricket is "...present in the lowlands of southern Pennsylvania; northern limits are in the vicinity of Philadelphia and Allegheny County. Occasional in deciduous woodlands, on oaks, but also on shrubs and vines. Appears adult in mid-August."

Fulton (1951, 6, Raleigh, North Carolina) gives the seasonal song period of this species as between about August 20 and November 20. In 1932, 6, he says it occurs mostly in bushes, vines, in or near woodland, and sings at night only.

Hebard (1934, 26) gives the northern limits of this species in Illinois as the towns of Hilliary and Quincy.

<u>Singing Behavior</u>

The song of this species has been heard more or less continuously throughout the seasonal song period at Columbus, Ohio.

*Franklin Co., O. (Clinton Twp.) (1) 21 Sept 1954, 65° F., 45 sec. (2) 49 sec. (3) 1 min, 26 sec. (4) 22 Sept 54, approx. 60° F., 10 sec., (5) 15 sec.

*Hocking Co., O. (Neotoma) 3 Sept 1954, 63° F., 35 sec.

*Piatt Co., Ill. (Sangamon Twp.) 4 Sept 1955 (1) 75° F., 16 sec. (2) 60° F., 23 sec. (3) 60° F., 17 sec.

<u>Song Description and Analysis</u>

The song of this species is the loudest of the cricket songs treated in this paper, except for that of <u>Gryllotalpa hexadactyla</u> Perty. It consists of a clear, continuous, musical trill, distinguishable from those of other tree crickets by its loudness, and by a deep, bell-like tone, one of the types of characteristics which are not shown on Vibragrams. The pulse rate at 65° F. is 33 per second, and the pitch is around 2 kilocycles per second (Plate XXXVIII).

All of the descriptions given by the following authors agree with that given here.

Allard (1910d, 6) Thompson's Mills, Georgia

Fulton (1915, 6, N. Y.). Pitched about third D# above middle C on warm summer nights — half note lower on cool nights.

<u>Oecanthus niveus</u> (DeGeer)

The Snowy Tree Cricket

<u>Introduction</u>

A great deal has been written about this species, chiefly because it was noted long ago (Dolbear, 1897, 6) that the approximate temperature in degrees Fahrenheit could be estimated by adding 40 to the number of chirps emitted in 15 seconds in the calling song. Since this species is one of the many singing insects which today occur in greater abundance in the "artificial" situations promoted and maintained in residential areas in towns and cities, or around country homes, than they do in "natural" or undisturbed areas, a great many people have "gotten into the act," attempting to apply Dolbear's formula in different parts of the country, and in experiments of varying reliability. For example, Faxon (in Edes, 1899, 6) concluded his calculations with the remark that if the thermometer had been on the same side of the house as the crickets, his results might have been somewhat different! Fulton (1925, 6) summarized the results of investigations on the chirp rate of this species conducted prior to that time, and also demonstrated the existence, in Oregon, of two "physiological races," varying, among other things, in their different chirp rates, but morphologically indistinguishable. Because of the interest in this species, and the large amount of published information, somewhat contradictory in some instances, it seems worthwhile to include a rather complete summary along with the findings of the present study.

Geographical Distribution

Fulton (1925, 6) states that this species occurs over most of the North American continent from Maine, Ontario, and British Columbia southward. He says it is uncommon in southeastern United States, but has been recorded from Cuba, Guatemala, and Mexico. Although he studied it in New York, Oregon, Ohio, Iowa, Colorado, and Arizona, and later in North Carolina (Fulton, 1932, 6, 1951, 6), he found evidence for the existence of two "races" only in Oregon.

The localities in which this species has been observed in the present study are recorded below. The record from Hoke Co., N. C., is apparently the only record from that general locality. The limits of distribution can be rather easily determined if one listens for the song while driving at night. Generally it will not be heard except when passing through the residential areas of towns, and if it is not heard in such areas, it is probably absent from the general locality.

Ecological and Seasonal Distribution

Of the two races he observed in Oregon, A (same as or similar to the eastern form) and B (known only from Oregon), Fulton states that A is strictly arboreal and B is predominantly a bush-inhabiting form, "...most common on prune, and apple and in the native growths of white ash and Gary oak. I have also heard it singing in cherry, maple, and poplar trees. It is usually more abundant among the higher branches and could be heard singing in the tops of quite large trees. The only berry bushes I have found it in were tall, coarse blackberries growing under trees." Of race B, Fulton says, "It is very common on loganberry and raspberry, and to a somewhat less extent, on blackberry. It occurs abundantly in the wild rose thickets... widely distributed though not abundant, among the brake ferns and associated plants in old burned areas in the Coast Range." Where the ecological ranges of these two forms came together along the edges of deciduous woods, Fulton occasionally found both singing in the same bush or small tree, but states that the extent of such contact was relatively small. The other differences which Fulton found in these two forms were in oviposition habits and song. He states (p. 379), "If its [Race B] differences from the other form where morphological rather than physiological, it would constitute a separate species."

Cantrall (1943, 6, George Reserve, Michigan) says, "Unlike angustipennis, niveus is often found in low shrubbery and tangles of vines. However, on the Reserve niveus is seldom taken in such situations owing to the scarcity of such environment and to the fact that most of the shrubbery is around the marshes and swamps. This tree cricket does not usually occur in these moist situations, except in the treetops, where humidity is lower. The tall shrub stratum of the oak-hickory woodland, however, harbors this species as abundantly as does the deciduous-arboreal stratum." He says the snowy tree cricket matures in late July and its song is often heard in early October, and does not completely die away until after heavy frosts have caused the leaves of the trees to begin dropping. "Light freezes often so chill these insects that they fall from the trees."

Hebard (1938, 6, Pennsylvania) says that this species prefers vines, apple trees, and bushes and appears adult in mid-July.

Blatchley (1920, 6, Indiana) says of this species, "...like other members of its genus niveus reaches maturity in southern Indiana about July 1st, and in the central part a fortnight later, and exists in that stage until after heavy frosts."

The observations carried out in the present study indicate that this species is an inhabitant of bushes and small trees, and is commonly encountered in apple and other fruit trees that are unsprayed. At the Ohio State University woodlot it occurs in the low trees and bushes along the border of the woods. Dense colonies often occur in isolated trees and bushes, and in brushy or vine-filled fencerows. At Bemis Woods in DuPage County, Illinois, it occurs in the bushes and small trees between a damp forest and a large permanent marsh. At Cedar Point, Ohio, on July 27, 1955, a rather unusual situation was encountered under a large ash tree standing alone near the water's edge along an inlet of Lake Erie. A cultivated field extended to within a few yards of the ash tree on the side away from the water, and a dense stand of cockleburr, blackberry, and sumac occurred all around the tree. Oecanthus niveus was singing in great numbers in the cockleburr, most specimens less than 3 feet above the ground. A few specimens occurred in the sumac and blackberry, but none could be heard in the tree. Nymphs of O. angustipennis were also abundant on the cockleburr and blackberry, which is the only time that I have observed this species in other than arboreal situations, although such habits have been recorded by other authors.

Singing Behavior

Neighboring individuals of the snowy tree cricket synchronize their chirps. In isolated, dense colonies this synchronization sometimes develops to such a degree that the whole colony is chirping together. A colony was observed in an isolated apple tree on the Ohio State University farm and it was noticed that synchronization did not become evident until sometime after singing began in the evening, and the whole colony did not develop synchrony until an hour or so after the beginning of song by the first individuals.

Some investigators have doubted that synchronization is effected in this species (Lutz, 1924,26), and others (Shull, 1907) have stated that synchronization "affects only 2 or 3 individuals near each other." Fulton (1928, 6) showed conclusively that synchronization is not merely an auditory illusion and that it occurs as a result of one individual hearing the song of another. He observed a cage of males before and after removing their tibial auditory organs. Before removal of their auditory organs these males synchronized their chirps. Afterwards, a completely asynchronous singing occurred. The distance between singers is probably a critical factor in this synchronization, as well as the length of time that the males have been singing. Lutz' observations may have been carried out early in the evening and Shull's observations may well have been conducted on scattered individuals, close enough for him to hear several individuals at once, but far enough apart, or perhaps so situated that all the individuals he could hear from his position, could not hear each other, at least not well enough to maintain synchrony.

Fulton (1925, 6) captured two male snowy tree crickets in Ohio and caged them with a pair of males from Grand Canyon, Arizona, and another pair of Oregon "A" males. He had already determined that the western specimens sang with a somewhat more rapid rate. He states, "When this lot was observed after dark, none of the usual synchronism of notes could be heard, but instead there was a confusion of sound, resulting from the crickets of each locality singing at somewhat different rates. One of the Arizona crickets was a most persistent singer, and would be the first to start after a disturbance. An Ohio cricket would then apparently attempt to start in unison, but after a few notes would lose cadence and stop. After several such attempts it would sing independently at a somewhat slower rate. Count of the three species taken within a half hour, with the temperature of the room holding close to 71° F., gave the following: Ohio 130, Arizona 140, Oregon A, 155."

Courtship has not been observed in this species.

Song Records

The song of *niveus* is common at Columbus, Ohio, and has been heard continuously throughout the singing season during the two years of this study.

*Franklin Co., O. (Clinton Twp.) 24 July 54, 63° F. (1) 57 chirps in 35 sec. (2) 20 chirps in 7 sec. (3) 28 July 54, 72° F., 122 chirps in 51 sec. (4) 53 chirps in 20 sec. (5) 25 Aug. 1954, 73 chirps in 30 sec.

*DuPage Co., Ill. (Bemis Woods) 18 Aug. 1954, 70° F., 41 chirps in 20 sec.

*Erie Co., O. (West of Berea) 26 July 1955, 76° F. (1) 51 chirps in 18 sec., (2) 88 chirps in 30 sec.

*Erie Co., O. (Cedar Point on cockleburr) 78° F., 26 July 1955, (1) 44 chirps in 14 sec. (2) 46 chirps in 15 sec. (3) 71 chirps in 25 sec.

*Bath Co., Va. (Warm Springs Mt.) 11 Aug 1955, 65° F., 63 chirps in 33 sec.

*Piatt Co., Ill. (Sangamon Twp.) 4 Sept. 1955 (1) 73° F., 139 chirps in 64 sec. (2) 58° F., 24 chirps in 15 sec. (3) 58° F., 50 chirps in 35 sec.

*DuPage Co., Ill., 9 Sept 1955, 78° F., (1) 50 chirps in 17 sec., (2) 42 chirps in 15 sec.

*Franklin Co., O. (Columbus) Borror (no temperatures recorded) (1) 12 Sept 1953, 87 chirps in 75 sec. (2) 18 Sept 1953, 140 chirps in 59 sec. (3) 10 Aug 1954, 80 chirps in 38 sec. (4) 22 Aug 1954, 246 chirps in 1 min. 27 sec. (5) 14 Sept 1954, 20 chirps in 9 sec. (6) 14 Sept 1954, 87 chirps in 71 sec.

Williams Co., O. (Northwest Twp.) 19 Aug 1954.

Piatt Co., Ill. (Sangamon Twp.) 29 Aug 1955.

Hart Co., N. C., 10 Aug 1955.

Carroll Co., O., 14 Aug 1954.

Song Description and Analysis

The song is rhythmical continuous repeating of clear, musical, relatively low-pitched chirps (2.5-3.0 kps.), at a chirp rate of 2-3 per second, as shown above. The pulse rate within each chirp, as shown in Plate XIII, varies from 30 to 60 per second in the temperature range of 58-78° F. The number of pulses per chirp varies from 5 to 10, but is most often 8. In the first specimen recorded by Borror above, apparently at a very low temperature, a few 2-pulse chirps occurred, though the rest contained 5-9 pulses. Usually the pulses are grouped in sets of 2-3, or 4, with a slightly longer interval between sets. The first 2 pulses are usually grouped together, and the 2-pulse chirps noted above apparently consisted of only this group.

Fulton (1925, 6) has summarized on scatter diagrams the results of Faxon and Edes in New England, Bessey in Nebraska, and his own results from Iowa and Oregon concerning the effect of temperature on chirp rate in this species. These diagrams show that for the "race" A, presumably the same species as that found all across the United States, the eastern specimens sing a little more slowly at the same temperature than do those from the west, with a gradual change occurring from New England to Oregon. In New England, Faxon got about 122 chirps per minute at 70° F., Edes got about 128, Fulton in Iowa got about 135, Bessey in Nebraska got 140, and Fulton in Oregon got 155. As has been mentioned, Fulton found that specimens from different parts of the range could not synchronize their chirps. Fulton's "race" A sang 90 chirps per minute at 70° F. The results of the present study are very close to Fulton's Iowa records, though the slope of the line is a little different, with the chirp rates varying in a linear or nearly linear relationship between 96 chirps per minute at 58° F. in Illinois to 184 chirps per minute at 78° F. in Erie Co., O.

Snodgrass (1924,26, Washington, D. C.) recorded 140 chirps per minute without giving the temperature, Dolbear (1897, 6) gave 80 chirps per minute at 60° F. and 120 per minute at 70° F. when he devised his formula, $T = 50 + \frac{N - 40}{4}$, or the temperature in degrees Fahrenheit is equal to the number of chirps in 15 seconds plus 40. Fulton (1915, 6, N. Y.) gave chirp rates between 64 and 155 per minute.

Pierce (1948, 26, Franklin, New Hampshire) found "about 8 pulses" per chirp, at a rate of fifty per second. The frequency of the sound he found to be 1222 cps., "with another nonharmonically related value of F = 2125 cycles per second." The chirp rate in his graph appears to be about 120 per minute.

Fulton (1915, 6, N. Y.) gives the pitch of this song as 2 octaves about middle C on warm evenings.

Summarizing the work on this insect, it appears that there are two species, one of which is limited to western United States and has not yet received a specific name (Fulton's Race B), and the other, Oecanthus niveus (DeGeer) which extends all across the United States and shows a clinal variation in the speed of chirping. These two species as yet cannot be distinguished morphologically, but where they occur together they occupy different habitats and have different oviposition habits.

Gryllidae, Trigonidiinae

The Sword-Bearing Crickets

Four species, in three genera, have been recorded in this subfamily. One or two undescribed species are involved. Only three species occur in Ohio, Indiana, and Illinois, with but one of these extending beyond the southern portions of these states.

All of these species overwinter in the egg stage and apparently have but one generation per season. Most species are commonly found on herbaceous vegetation within a few feet of the ground and sing both day and night, while the single species restricted to trees sings only at night.

Apparently no one has observed copulation closely enough in species of this subfamily, or examined the males to see if a metanotal gland exists which is attractive to the female. The tegmina are held at a 90° angle, as in the Oecanthinae, both during the calling song, and during courtship in at least one species (*Anaxipha exigua* (Say)). This is the only species that has been observed in courtship, and it has a well-defined courtship song, unlike any of the *Oecanthinae*.

The songs of the species in this group are very high-pitched, clear trills or chirps, that are not very loud to human ears because of their high frequency. Only one species chirps, and the individuals in this species synchronize their songs.

One species in this subfamily, *Falcicula hebardi* Rehn, has apparently lost both its ability to produce and perceive sound. Fulton (1932, 6) found 30 faint cross ridges on the stridulatory vein, but it has never been heard to sing, and according to Fulton its tibial auditory organs have completely disappeared.

Anaxipha exigua (Say)

Say's Bush Cricket

Introduction

Fulton (1951, 6) has described three "song forms" in this species. Two of these occur in Ohio, and are believed to be distinct species. They are separable by size, song, and ecological distribution, and one is limited to the southern portions of the state. Fulton's "triller" is the species treated here under *Anaxipha exigua* (Say), his "fast tinkler" is probably the same as the species treated here as "Anaxipha (undescribed species)." His "slow tinkler" apparently does not occur in Ohio. Dr. Fulton now has a paper in press (Journal of the Elisha Mitchell Scientific Society) in which he discusses these three forms in detail.

Distribution

Say's bush cricket (Fulton's triller) apparently occurs all over the area studied. At Columbus, Ohio, the calling song is heard from mid-July until heavy frost. This cricket is an inhabitant of damp lowland areas of all kinds, occurring on sedges over open water, in open areas in swamp forest associations, along stream banks, and along roadsides and fencerows in poorly-drained areas.

Fox (1917, 6, Virginia) found exigua in a tidal marsh (Sept. 9). Cantrall (1943, 6, George Reserve, Michigan) records adults between July 20 and late September and found it to be a characteristic species of the "wet shrub zone habitat."

Singing Behavior

Singing males are usually found within 3 feet of the ground, sometimes only a few inches above the ground in short grass. Occasionally they will be perched 4 or 5 feet above the ground in tall vegetation such as in cattail marshes. Individual singers are very difficult to locate because of the piercing quality of the very intense, high-pitched song. As a male is approached he stops singing, but due to the ear-filling quality of the singing of the entire colony, the observer often does not notice this and continues on to the next singer. This is especially true in very dense colonies.

This species holds the tegmina at an approximate 90° angle with the body, both during the calling song and during courtship. The female was never observed to mount, but it is presumed that the copulatory position is like that in the Oecanthinae. It is not known whether the male has a female-attracting metanotal gland, but a point of interest is that this is the only species observed which holds its wings in this position and has a rather well-defined courtship song. No male encounter or "fight" sound has been heard.

Song Records

*Franklin Co., O. (University Woods) (1) 25 Sept 1954, 75° F., 55 sec. (2) 7 Sept. 1954, 85° F., 54 sec. (calling and courtship songs).

*DuPage Co., Ill. (Bemis Woods) 18 Aug 1954, 53 sec. (temperature unknown).

*Coshocton Co., O. (Nellie) 27 July 1954, 85° F., 3 min. (courtship song).

Dickenson Co., Va., 6-7 Aug 1955.

Raleigh, N. C., 8-9 Aug 1955.

Hocking Co., O. (Neotoma), 3-4 Sept 1954.

Piatt Co., Ill. (Sangamon Twp.), 29 Aug 1954.

Pickaway Co., O. (Circleville), 26 Sept 1954.

Licking Co., O., 15 Sept 1954.

Columbus, Ohio, July 17-September 29 (1954 and 1955 combined).

Porter Co., Ind., 19 Aug 1954.

Song Description and Analysis

The calling song is a very high-pitched, rapid, continuous trill. It is a very intense and clear sound, but because of its high pitch (about 7 kps.), it is not loud to human ears, and is very difficult to locate. The pulse rate is about 36 per second at 75° F. (Plate XLI).

The courtship song, heard on a number of occasions in the field, and observed in males backing toward females in laboratory cages, is the same sound, but produced in a short regular burst slightly more than a second in length (Plate XLII), and delivered at rates of from 2-3 in five seconds. Each burst (or short trill) becomes louder toward its end. As with most courtship songs of crickets, this song is accompanied by jerking motions of the body.

The calling song of this species has been described by Allard (1910b, 6, Thompson's Mills, Ga., and 1929, Washington, D. C.) and Cantrall (1943, 6, George Reserve, Michigan). These descriptions agree in general with that given above, or are not complete enough to adequately compare. Allard (1929c, 6) describes a spring "brood" during May and June and a later brood which is present in the adult stage from July to frost. The two differ also in song and in habitat, with the spring brood occurring in moist situations and near the ground, and the summer brood occurring on shrubs and even low trees. It is probable that he was describing the triller and the fast tinkler, the two forms treated here.

PLATE XLI.

CALLING SONGS OF TRILLING TRIGONIDIINAE

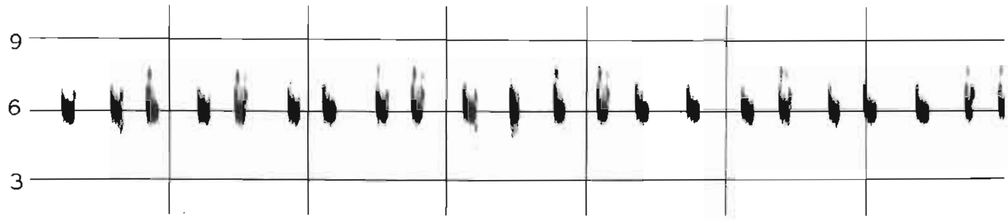


Fig. 108. PHYLLOPALPUS PULCHELLUS APPROX. 80°F.

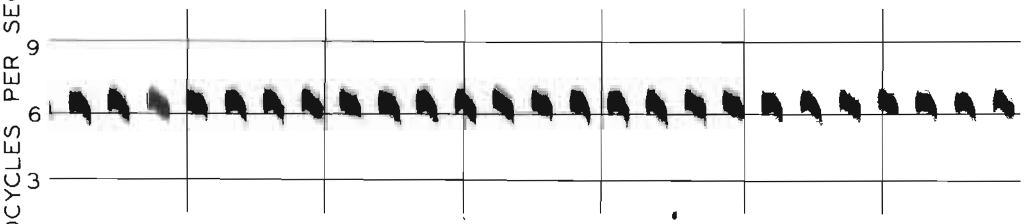


Fig. 109. ANAXIPHA EXIGUA (TRILLER) 75°F.

FREQUENCY IN KILOCYCLES PER SECOND

Fig. 110. ANAXIPHA EXIGUA (FAST TINKLER) 74°F.

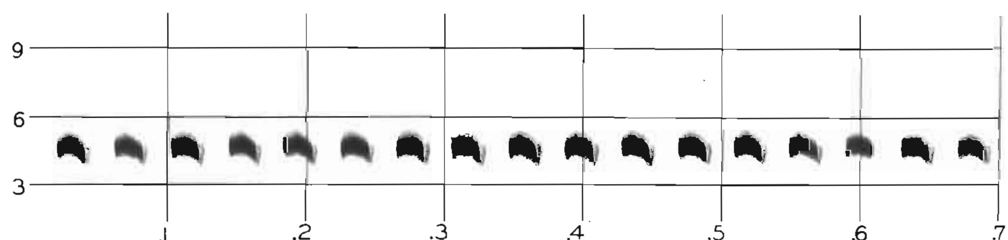


Fig. 111. ANAXIPHA (?) UNIDENTIFIED APPROX. 70°F.

TIME IN SECONDS

PLATE XLII. COURTSHIP SINGING IN CRICKETS WITH METANOTAL GLANDS

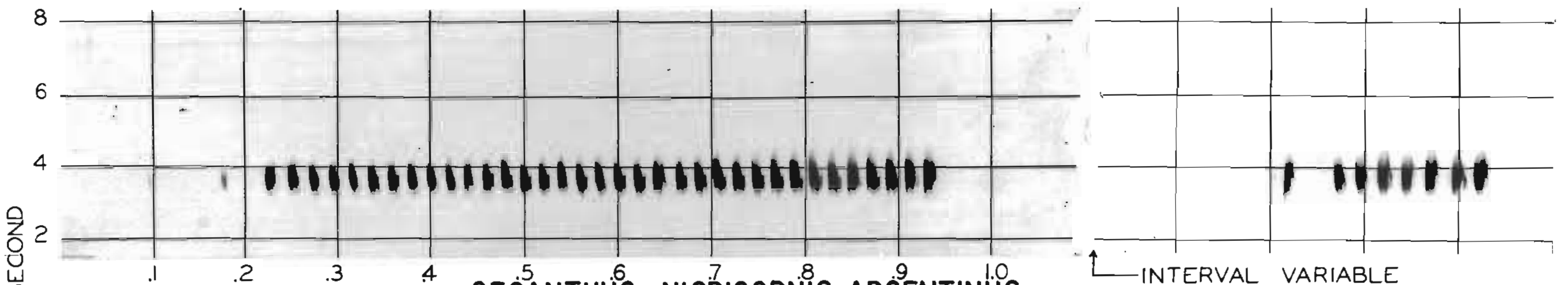


Fig. 112. OECANTHUS NIGRICORNIS ARGENTINUS

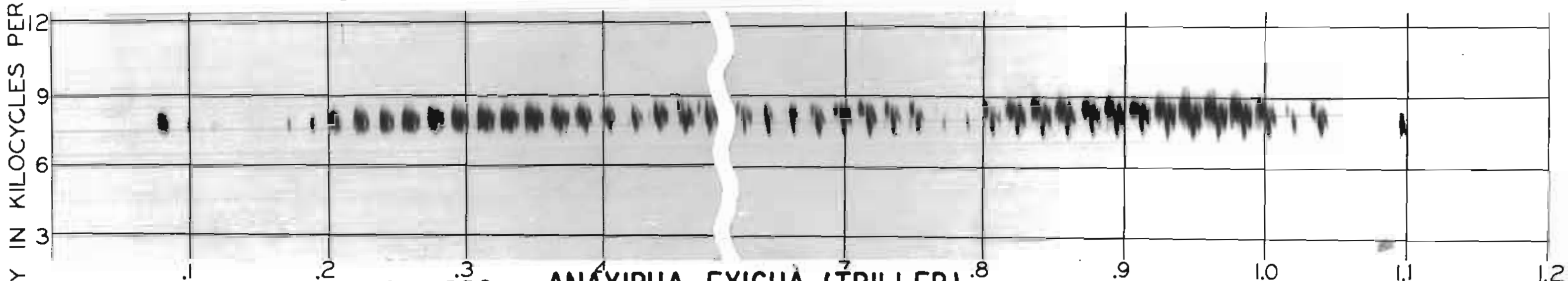


Fig. 113. ANAXIPHA EXIGUA (TRILLER)

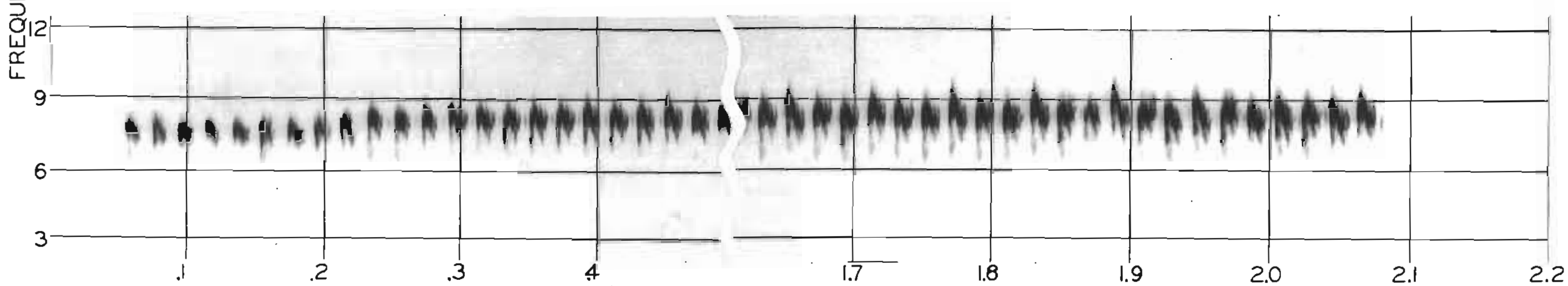


Fig. 114. ANAXIPHA EXIGUA (TRILLER)

TIME IN SECONDS

Anaxipha (undescribed species)

Fast Tinkler

Distribution

This species was discovered in Ohio by Dr. Edward S. Thomas who pointed it out to me. Dr. Thomas sent a series of specimens to Dr. Fulton whose paper on *Anaxipha* is in press. Fulton was unable to find morphological characters to separate it from *exigua*, but in Ohio these two species are separable by size, *exigua* being considerably larger than this species.

This species is presumed to be the same as Dr. Fulton's "fast tinkler." The ecological distribution of the fast tinkler seems like that of the present species, and the song sounds identical. I heard the fast tinkler once at Raleigh in August, when it was pointed out by Dr. Fulton. Fulton gives the song period of this form as from just past mid-July to December 1 at Raleigh, North Carolina.

In Ohio this cricket is limited to the southern portion of the state; I have observed it only in Hocking County, at Neotoma. It occurs on dry hillsides, in pine or on various kinds of bushes and weeds. At Neotoma it was heard on weeds around a cabin within 2 feet of the ground, and in pine trees 6-8 feet above the ground. A large number of individuals were spotted with a flashlight at night in a pine tree, about 7-8 feet above the ground. Both sexes were in the tree, and one female was apparently ovipositing in a branch about 2 inches in diameter. In Dickenson County, Virginia, this species was heard, recorded, and collected in the pine mountains. Eleven out of twelve individuals heard singing in an open, primarily deciduous forest, were found on the scattered small pines in the area. Only one individual was heard on something other than pine (sumac).

Singing Behavior

Only the calling song has been heard. The tegmina are held in approximately a 90° angle during this song.

Song Records

*Hocking Co., O. (Neotoma) 4 Sept 1954 (temperature unknown, estimated at 80-85° F., 2 min. 28 sec., 8 breaks, 19.3 pulses/sec.

*Dickenson Co., Va. (Pine Mts.) 6-7 Aug 1955, 73 sec., 7 breaks, 15 pulses/sec.

Song Description and Analysis

This song is a continuous trill, like that of *N. exigua*, but with the pulses produced at a much slower rate, 19.3 per second at 80-85° F. The frequency is somewhat higher (about 8 kps.), as would be expected due to the smaller size of this species. The structure of the individual pulses in this song is identical to those in the song of *exigua*, or very nearly so; the chief difference in the songs is that the length of the interval between pulses is expanded. The similar length of pulses and pulse intervals in the song of *exigua* indicate that the wing motion involved is of the "open - close -

hold - open - close - hold." Thus the songs of these two closely related species differ only in the introduction of an interval during which the wings are held motionless. The "slow tinkler" (Fulton, 1951, 6) apparently has only lengthened this "hold" period. The same relationship exists between the songs of Nemobius fasciatus and N. tinnulus, and between the calling and courtship songs of each of those two species.

An Unknown Gryllidae

(Possibly Anaxipha sp.)

On August 14 and 15, 1954, Dr. E. S. Thomas and I heard a song which neither of us recognized, coming from the base of clumps of the common rush in Specht Marsh in Carroll County, Ohio. Although both of us searched for hours, neither succeeded in capturing, or even seeing a single specimen. The song was recorded and is discussed and analyzed below. It was produced both day and night.

On June 15, 1955, at Giant City National Park and near Wolf Lake in southern Illinois, I heard a song from cattail marshes which at first did not impress me as familiar except that at low temperatures in the evening, it sounded very much like the calling song of Oecanthus quadripunctatus. The singers proved to be an Anaxipha which I was unable to identify. Fulton saw the specimens and expressed the opinion that they were Anaxipha delicatula Scudder, though this locality was considerably outside the range of that species. The song which Dr. Thomas and I heard in the Carroll County marsh and is here described and analyzed may have been the same. I did not have a tape recorder along in Illinois and the specimens I brought back alive died without singing in the laboratory.

Song Description and Analysis

The song is a clear, continuous trill, slower and lower-pitched than the other *Anaxipha* described here, and in pitch it is near *Nemobius* spp., somewhat intermediate between *Acheta* and Anaxipha. As seen in Plate XLI, the pulse rate at 70° F. is about 25 per second, and the frequency is around 4.5 kps.

Cyrtoxipha columbiana Caudell

Caudell's Bush Cricket

This cricket was encountered from Pike County, Kentucky, south-to Raleigh, North Carolina, on an early August trip through that area in 1955. It is a night-singer, beginning in late afternoon, and according to Fulton (1951, 6) sings from mid-July to early October at Raleigh, North Carolina. It occurs in bushes and trees, generally 6 feet or more above the ground (Fulton, 1932, 6). Its wings are lifted to a 90° angle during song, and the individuals of a colony synchronize their chirps much as do the individuals in a colony of *Oecanthus niveus*.

Song Records

*Pike Co., Ky., 6 Aug 1955 (temperature not recorded), from

3 P. M. into the night, 1 min. 46 sec. at 280 chirps/min.

*Lenoir, N. C., 2 Aug. 1955, 4:40 P. M. (temperature not recorded) 110 chirps in 36 seconds.

*Raleigh, N. C., 8 Aug. 1955, 79° F. (1) 35 sec. at 210 chirps/min. (2) 2 min., 35 sec. at 208 chirps/min.

Song Description and Analysis

This song is a continuous repeating of clear, high-pitched chirps at a rate of 3-4 per second. Each chirp contains 5-6 pulses delivered at 40 per second, and the sound is pitched at around 8.2 kps. Although the chirping rate is regular and rhythmical, there are often gaps as though a single chirp had been left out.

Phyllopalpus pulchellus Uhler

The Handsome Bush Cricket

Distribution

This is a southern species, reaching only to northern Hocking County in Ohio. In Illinois, according to Hebard (1934, 26), it extends to Monticello in Piatt County. From Ohio south to Raleigh, N. C., it is heard almost continuously along the roadsides, especially on dry hillsides, along forest borders, and in brushy and weedy areas of various kinds. At Circleville, Ohio, I have heard it in the bushes along a swamp forest border, and in Pike Co., Ky., it was singing in numbers on August 6 in giant ragweed along a small creek.

In Ohio I have heard this species only between Aug 20 and Sept 15, but this is certainly not its complete song period. Fulton (1951,6) gives its song period at Raleigh, North Carolina, as late July to October. According to Hebard (1938, 6) adults appear in late July in southeastern Pennsylvania. Blatchley (1920, 6) says adults appear in mid-August in southern Indiana.

Singing Behavior

This cricket is usually found within 2-4 feet of the ground, and it sings both day and night. At night its soft, creaky song is almost completely obliterated by the loud noises of other species, and it is probably most noticeable late in the afternoon before the night-singers start.

Song Records

*Hocking Co., O. (Neotoma) 4 Sept 1954, 80-85° F. (estimated) 1 min. 12 sec.

*Pickaway Co., O. (Pickaway Twp.) 10 Sept 1954, 75° F., 1 min. 33 sec.

Ironton, O., 26 Aug 1955, Lawrence Co., Ky., 6 Aug 1955, Pike Co., Ky., 6 Aug 1955, Raleigh, N. C., 8 Aug 1955, Bath Co., Va., 11 Aug 1955.

Song Description and Analysis

This song is a continuous, sputtery, high-pitched trill (30 pulses per second at 80° F.), less musical than any other cricket song treated in this paper. It is pitched at about 6 kps. and is not very loud, but is noticeable several yards away. Fulton (1932, 6) described it as resembling the sound produced by a wooden Halloween rattle twirled on a stick, and this is a very good comparison. I correctly identified by its song the first specimen I ever heard before I had seen it, as a result of reading Fulton's description 3 or 4 months before.

The descriptions given by Allard (1910b, 6, Thompson's Mills, Ga.) and Fulton (1932, 6, Raleigh, N. C.) agree with that given here.

Gryllidae, Mogoplistinae

The Wingless Bush Crickets

Little is known of the singing habits of the species in this group, and apparently nothing of their courtship and copulatory behavior. According to Fulton (1932, 6) all but one of the four species which he observed sing only at night; he says of the fourth "...sings to some extent in the daytime." All of these species occur in low vegetation or in leaf litter on the forest floor. They apparently have but one generation per season, and since they begin singing around mid-August, presumably overwinter in the egg stage.

These are tiny insects only a few millimeters long, and the tegmina of the males scarcely extend beyond the pronotum, much like those in the Decticinae. It seems incredible that they can make any audible noise, and as would be expected the sound is very high-pitched and faint.

Only one species has been observed in this study, and only on one occasion.

Cycloptilum bidens Hebard

This cricket was recorded and collected at Crab Orchard State Forest north of Raleigh, North Carolina. It was identified by Fulton's description of the song and habitat (1932, 6). He gives its song period as from early August to November 1, and describes its habitat as among leaves or low undergrowth of woodland, most common in pine woodland, and says it sings to some extent in day-time. The specimens we recorded and captured were singing at night only a few inches from the ground on dead twigs and leaves in a dense woodland.

Song Records

*Raleigh, N. C., 8 Aug 1955 (1) 76° F., 12 partial chirp sequences in 2 min., 25 sec., 9-60 chirps per sequence (2) 15 Aug 1955, 85° F., 15 chirp sequences in 3 min., 26 sec., ranging in length from 2 to 36 chirps (when disturbed, chirp sequences shorter), 3 chirps per second in steady chirping.

Song Description and Analysis

The song is a series of 30-60 brief, weak, high-pitched, double-pulse chirps repeated at rates of 2-3 per second. The series is repeated after a few seconds break. Fulton's (1932, 6) description says, "faint, brief notes like a light tap on one of the high keys of a xylophone." The pulse rate is around 60 per second, and the frequency of the sound about 8.2 kps. at 85° F.

Gryllidae, Eneopterinae

The Larger Brown Bush Crickets

This is an interesting subfamily since, in addition to species with well-developed sound production, it contains at least one species apparently in the process of losing both its ability to produce and perceive sound. Several specimens of this species, Hapithus agitator Uhler, were collected and kept in the laboratory for several weeks, but were never observed to stridulate or copulate. Fulton observed a male in stridulation on one occasion; his observations and others made in the course of this study are discussed on page 62.

Only one species in this subfamily has been recorded in the present study.

Orocharis saltator Uhler

The Jumping Bush Cricket

Distribution

This species is southern, extending continuously to at least Pickaway Township in Pickaway County and to northern Hocking County in central Ohio. A colony is located along Alum Creek on the eastern edge of Columbus, and another along the Olentangy River west of Columbus (Dr. E. S. Thomas). Apparently both of these colonies extend north beyond Columbus; Dr. Thomas has traced the Olentangy River colony into Delaware County. The Alum Creek colony has been known to Dr. Thomas for a number of years, apparently has survived through several severe winters, and is presumably permanent. This species may be transported in the egg stage on shrubbery and trees which would explain its frequent appearance in colonies in inhabited areas outside its "continuous" range. In 1955, a single specimen was heard singing on the Ohio State University Campus, though none had ever been heard there before, or within several miles of the campus.

This cricket has been heard in damp forests and along stream banks, and at Ash Cave in Hocking County, Ohio, where it is especially abundant, it extends up the slopes of the ravine to near the ridge-top.

The colonies at Columbus have been visited only during September. Fulton (1951, 6) gives the song period at Raleigh, N. C., as from mid-August to December 1, and in 1932, 6, he says that it occurs in vines, bushes, and trees.

Singing Behavior

Singing males are found in bushes and trees, 4-5 feet to 20-30 feet above the ground, depending on the situation. In spite of their rather large size, these insects are extremely difficult to locate, partly because their song is discontinuous, and has a ventriloquistic effect, and partly because of their inconspicuous appearance due to a camoflaging mottled brown coloration, and their habit of flattening themselves against their perch. On several occasions I have had my face within a few inches of a singing male for several minutes before finally locating him by catching the movement of his tegmina.

Singing is done at night only, and neighboring males seem to alternate their chirps, though it is difficult to determine whether this is an auditory illusion. Courtship and mating have not been observed. The wings are held in the calling song in the 90° angle position characteristic of the Oecanthinae and Trigonidiinae. It is apparently not known whether a female-attracting gland is present on the metanotum.

Song Records

*Hocking Co., O. (Neotoma) 3 Sept 1954, 63° F., 20 chirps in 175 sec.

*Franklin Co., O. (Mifflin Twp.) (1) and (2), 11 Sept 1954, 80° F., 47 sec. (chirping together), (3) 25 chirps in 45 sec.

*Hocking Co., O. (Ash Cave) 11 Sept 1954, 65° F., 12 chirps in 34 sec.

*Pickaway Co., O. (Pickaway Twp.) 10 Sept 1954, 63° F., 13 chirps in 31 sec.

*Chesterfield Co., Va. (Thomas Walker) 13 Sept 1955, 59° F., several specimens, 20 sec.

*Dyar Co., Tenn. (Walker) 24 Sept 1955, 67° F., 12 chirps in 27 sec.

Song Description and Analysis

This song is a loud, "piping" chirp, very clear and musical, repeated continuously at a rate of about 1 in 2 seconds. As shown in the following table the chirps contain 7-17 pulses delivered at rates of 31-50 per second between 63° F. and 80° F., and the sound has a frequency of from 3.5 to 5.7 kilocycles per second, depending also on the temperature.

Table 6

Analysis of Song Characters in Orocharis saltator

Temperature	Pulses per Second	Frequency in kps.	Pulses per Chirp
63° F.	31	4.2	17
80	50	5.4	11
60	50	5.7	13
63	30	3.5	16
80	50	5.2-5.4	9
59	35	3.5	7
67	43	4.8	13

These figures were taken from the above recordings in the same order that they are listed, by analyzing a Vibragram of one chirp from each song. Each chirp is characterized by a slight rise in pitch, about 200-400 cps. from beginning to end. In one chirp the frequency change was from 5.2 to 5.4 kps. in 7 pulses.

This song has been described by the following authors whose descriptions largely agree with that given above:

Snodgrass (1923, 6, Washington, D. C.).

Allard (1910b, 6, Thompson's Mills, Ga.) and 1928a, 6, probably Washington, D. C.) probably 6 pulses per chirp and 35-40 chirps per minute.

Fulton (1932, 6, North Carolina) 5-8 chirps in 10 seconds.

Gryllidae, Gryllotalpinae

The Mole Crickets

Sound production and associated behavior in this group is unique for several reasons. The mole crickets are the only crickets in which the female is known to possess stridulatory organs and to make a sound, though this is not at all uncommon in the Tettigoniidae. Baumgartner (1905, 26, 1910, 26) conducted a number of excellent observations on Gryllotalpa in Kansas (Species not indicated). He discovered that the tegmina of the female possessed stridulatory structures similar to those of the male, and later heard the chirping of a female. "The female mole cricket has quite a loud and distinct chirp. It usually consists of a single note; but there may be several at short intervals. This note is less shrill than the ordinary call of the male. However, the male has a note very similar to that of the female which it uses for the same purposes, namely, as a means of recognition in the dark burrows. The call is always given when one individual is approaching another, especially when digging a new tunnel."

Apparently Baumgartner is the only investigator to observe copulation in Gryllotalpa. His account is as follows:

> The courting is somewhat similar to that in Gryllus. The male calls the female with loud, long chirps. As she approaches the chirps become short and much softer. He then frequently turns his abdomen towards her. As the pair get ready to copulate the position assumed is quite different from that of any other animals of which I know. They turn posterior end to posterior end, and ventral side to ventral side, so that the cloacal openings are just opposite each

other. The female stands erect with her abdomen slightly raised, while the male lies on his back. The abdomens are tightly held together by hooks, described with great detail by Peytoureau. The sperm were carried to the female by a spermatophore. The time it takes for the transfer is not over a minute; but the pair kept their relative position, the abdomens simply touching each other, for more than ten minutes. After disturbance the male followed the female and again assumed this relative position, but no further transfer of a spermatophore occurred.

As the vesicle was being transferred, or just after it had been put in place, there was an outflow of some transparent fluid on either side of the vesicle. This soon hardened.

The copulatory position described by Baumgartner is apparently very similar to that assumed by the Dermaptera. Fulton (1924, 26) has described the copulation of the European earwig, _Forficula auricularia_ L., as follows:

The male does not use its forceps as claspers at any time during the act. After he has located a female with his antennae, he turns around and tries to slip the forceps under the tip of the female's abdomen. At this time the two are facing in opposite directions. It is then necessary for him to twist the body around so that the two ventral surfaces are together, the ends of the abdomens touching, the forceps of each extended along the ventral side of the other's body. In this position coitus takes place and lasts usually for a matter of hours, if the insects are not disturbed.

In my large breeding cages, the earwigs were usually clustered together in the corners. In mating the male usually stood on one side of the corner and the female on the other. This required the male to twist his body only ninety degrees instead of half a revolution as would be necessary if they were both on the same surface. In nature the earwigs always seek a narrow crevice in which to hide. I supplied them with a retreat of this kind, made of two pieces of glass covered with wire screen, with a quarter inch space between. In this a number of pairs were observed in coitus, but always with the male clinging to one surface and the female to the other so that no twisting of the body was necessary. This is probably the normal position.

The similar copulatory positions of the Dermaptera and Gryllotalpinae may be correlated with the fact that they both live in restricted areas, crevices and burrows. The upside-down position of the male seems difficult to explain since it would seem easier to derive a simple end-to-end position from the head-to-head, female-above position characteristic of the Gryllidae. However, in the Tettigoniidae which assume an end-to-end position in copulation, Turner (1916, 26) says the abdomen of the male is twisted 180°.

The flow of fluid following the transference of the spermatophore in Gryllotalpa is suggestive of that occurring in the Tettigoniidae.

Only one species of Gryllotalpinae has been recorded in this study.

Gryllotalpa hexadactyla Perty

The American Mole Cricket

In this study this cricket has been heard only in Pickaway and Champaign Counties in Ohio, on three occasions between July 30 and September 19. Fulton (1951, 6) gives its song period for Raleigh, North Carolina, as from mid-July to November 1, and suggests that the females may live through the winter, the males being present only during the song period, then dying in late fall or winter. He suggests that this species may have a two-year life cycle with the eggs laid in the spring or early summer and the nymphs maturing in the following summer.

Hebard (1938, 6, Pennsylvania) says that the adults are present from early spring to late fall. Cantrall (1943, 6, George Reserve, Michigan) states that the song was heard from July 24 to September 24. Hubbell (1922, 6, Michigan) found immatures from June 29-July 2, and September 1-3, adult males on September 1-3, and an adult female on August 17. The nymphs he took in September were young while those taken in late June and early July were nearly mature.

This species sings from the entrance of its burrows in wet, muddy areas along stream banks, particularly in marshy areas where the soil is nearly saturated. Only one male was captured in this study, though the burrows from which several others were apparently singing were dug out to below the water level. The male captured was approached on a mud flat while he was singing. He stopped when we were 3 or 4 yards away. Noticing the entrance to his burrow I ran quickly forward and dug out a large chunk of mud containing perhaps the upper foot of his burrow. The cricket was found inside this chunk of mud. He was kept alive for several days in the laboratory, but did not sing.

Hubbell (1922, 6) found nymphs numerous in the saturated sandy margins of a pool on a springy hillside, and 3 adult males were found singing in a small chamber about 1 inch below the ground surface in a low, moist pasture.

Singing Behavior

On the three occasions that I heard this species, it began singing at dusk and continued into the night. Cantrall says he also heard it during cloudy days, and Fulton says that this species sings day and night.

This species is apparently unique in that it has a chirping song which is quite rhythmical (steady in rate), with from 1-2 chirps delivered per second, yet different individuals neither synchronize nor alternate their songs. In most species which have uniform or rhythmical repetition rates below 3 per second, neighboring individuals either synchronize or alternate their songs.

Song Records

*Champaign Co., O. (Cedar Swamp) 24 Aug 1954, 70° F. (bulb of thermometer just submerged in mud), (1) 57 chirps in 30 sec. (2) 448 chirps in 4 min., 15 sec.

Champaign Co., O. (Cedar Swamp) 30 July 1955; Pickaway Co., O. (Pickaway Twp.), 10 Sept and 19 Sept 1954 (Specimen collected).

Song Description and Analysis

The song consists of a regular or rhythmical repeating of loud, low-pitched, "gutteral" chirps at a rate of about 100 per minute at 70° F. (Plate XXXIII). It is a clear, musical sound, and the lowest-pitched cricket sound known. It can be heard at considerable distances, probably up to 300-400 yards under favorable conditions, and is often incorrectly attributed to a frog, because it is heard along stream banks and is so loud and low-pitched. Chirping is continued for long periods of time without pause.

This song has been described by the following authors:

Scudder (1893, 6) "...a gutteral sound like grii or greeu, repeated in a trill indefinitely but seldom for more than two or three minutes and often for less time. It is pitched at two octaves above middle C and the notes are usually repeated at the rate of 130-135 per minute, sometimes, when many are singing, even as rapidly as 150 per minute. Often when it first begins to chirp it gives a single prolonged trill of more slowly repeated notes, when the composite character of the chirp is more readily detected."

Morse (1920, 6, New England, Tennessee): " a low-toned querr, querr, or gruu, gruu..."

Blatchley (1920, 6, Indiana): "...a sharp, disyllabic chirp continuously repeated and loud enough to be heard several rods away."

Snodgrass (1923, 6, Washington, D. C.): "...churp, churp, churp repeated very regularly about a hundred times a minute and continued indefinitely if the singer is not disturbed."

Fulton (1932, 6, North Carolina): 2-3 notes per second; loud, clear, rhythmical, but not synchronized.

Cantrall (1943, 6, George Reserve, Michigan): 3-5 notes per second, at 86° F., synchronized exactly with a colony of Oecanthus niveus.

Table 7

Analysis of Recorded Songs of <u>Gryllotalpa hexadactyla</u>

Temperature	Average Chirp Rate	Pulses per Chirp	Average Pulse Rate
70° F.	1.9/sec.	10-14 (av.11.73)	64.3/sec.
70° F.	1.76/sec.	8-19 (av.14.1)	64.9/sec.

In 22 pulses in 2 chirps of specimen 1, there were 5-17 tooth strikes per pulse, with an average of 12.55. The tooth strike rate was 1640 per second, which corresponds roughly to the frequency of the sound. The frequency of certain chirp lengths in these two recordings is shown below.

Table 8

Number of Pulses per Chirp in <u>Gryllotalpa hexadactyla</u>

Specimen 1		Specimen 2	
No. of Pulses	No. of Chirps	No. of Pulses	No. of Chirps
10	6	8	1
11	17	9	0
12	20	10	2
13	12	11	2
14	1	12	3
		13	7
		14	16
		15	8
		16	5
		17	4
		18	1
		19	1

A COMPARATIVE STUDY OF SOUND PRODUCTION IN INSECTS, WITH SPECIAL REFERENCE TO THE SINGING ORTHOPTERA AND CICADIDAE OF THE EASTERN UNITED STATES

Volume II

DISSERTATION

Presented in Partial Fulfillment of the Requirements
for the Degree Doctor of Philosophy in the
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University

By

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Tettigoniidae, Phaneropterinae

The Bush and Round-Headed Katydids

All of the northeastern species in this group have been recorded in this study, with the exception of the northern bush katydid, Scudderia septenrionalis (Serville). This nocturnal and arboreal species was neither heard nor collected during the study. Its song has been described by Hebard (1945, 6) and Cantrall (1943, 6). Their descriptions are similar. Cantrall says the song is composed of 2 phases, a series of 6-8 or more ticks (probably individual tooth-strikes) followed by 6-8 "clear, brisk notes...dee-dee-dee-dee-dee-dee." (Apparently each caused by a complete wingstroke).

The katydids in this group all have one or less generation per season, and overwinter as eggs. In some (Amblycorypha oblongifolia (DeGeer) Hancock, 1916, 26), the eggs may take 2-3 years to hatch. Apparently mating has been described for none of the species treated here, and courtship for only one species (Scudderia furcata furcata Brunner, Fulton, 1930, 6). In this case the female mounted the male under his lifted tegmina, mouthing the dorsal surface of his abdomen as do the females of crickets and cockroaches known to possess female-attracting glands on the metathorax or the abdomen.

Isely (1941, 6) describes mating in several species of Phaneropterinae in the genera Dichopetala, Arethaea, and Amblycorypha, indicating that the female mounts the male under his lifted tegmina, the male seizes the female near the base of the ovipositor with his forceps-like cerci, and the two remain in this position for from a few moments (Arethaea ambulator Hebard) to several hours (Dichopetala emarginata Brunner). Turner (1915, 26) describes mating in Ceuthophilus latens as end-to-end, and states (1916, 26) that this is the usual method of copulation in the Tettigoniidae. Baumgartner (1907, 26) describes copulation in a "Diastrammena" introduced from Japan (apparently Tachycines asynamorus Adelung), and says that the female mounts on the back of the male.

Most species in this group sing only at night, though certain species of Scudderia have distinctive songs that are produced in the daytime, according to Scudder (1868, 6) and Cantrall (1943, 6). The males are sedentary, perching more or less horizontally during song, either on tall herbaceous vegetation or in trees. The songs are various combinations of ticks and lisps, produced by individual tooth-strikes and wingstrokes, respectively, and ranging from simple lisps to the longest and most complicated song known in North American insects (Amblycorypha uhleri Stal). None of the eastern species synchronize their songs, though alternation occurs in several species. Synchronization has been described for western species of Amblycorypha (Fulton, 1928, 6; Isely, 1941, 6).

Scudderia pistillata Brunner

Broad-Winged Bush Katydid

Distribution

This katydid is northern in distribution, extending, according to Rehn & Hebard (1914, 6), from Halifax, Nova Scotia, southward to Chester in northern New Jersey, and westward as far as Regina, Saskatchewan, and Bozeman, Montana.

In the present study it has been heard on only three occasions, between July 26 and August 19, in marshy areas in northern Illinois and Ohio. Blatchley (1920, 6) records adults August 13-October 7, about peat bogs and lake borders in Steuben, Fulton, and Kosciusko Counties, Indiana. Hubbell (1922b, 6, North Dakota) found adults between July 19 and August 25, among bushes and tall herbaceous vegetation in the margins of woods bordering lakes and streams, in brushy clearings, roadside thickets, and meadows of tall herbage. In 1922, in Michigan, Hubbell found adults from July 18 to September 7 in second-growth scrub, roadside thickets of low bushes and tall weeds, in sedge and lizard's tail marshes, and in a cranberry bog. Hebard (1938, 6, Pennsylvania) says adults appear in early August and are found on bushes in pastures or open areas in northern swamps and forests. Cantrall (1943, 6, George Reserve, Michigan) found adults from July 13-August 29 in the "wet shrub-zone habitat," and one male in the "mixed grass-herbaceous habitat."

Singing Behavior

This species has been heard only at night in the present study, beginning shortly after sundown or in early dusk. Cantrall (1943, 6) says that the day song is the same as that of texensis and curvicauda, and differs from the song produced at night. Singing males perch more or less horizontally, generally on the tallest herbaceous vegetation in the area, usually from 2-6 feet above the ground. The song is sometimes repeated at about 5-second intervals, with longer gaps of a minute or more between such series. At other times, a single song or phrase is produced, with a minute or more elapsing before the next phrase. No observations on spacing, sedentariness, or social stimulation have been carried out.

Song Records

*Champaign Co., O. (Cedar Swamp) 24 Aug 1954, 73° F., 1 min. 36 sec., 4 phrases or songs, at 0 sec., 1 min., 1 min. 13 sec., and 1 min. 18.5 sec., containing 9, 7, 9, and 9 pulses respectively, with a pulse rate of 18 per second.

DuPage Co., Ill. (Bemis Woods) 18 Aug 1954, 70° F.

Williams Co., O. (Northwest Twp.) 19 Aug 1954.

Song Description and Analysis

This song is a multi-pulse phrase in which the individual pulses (lispy notes) are delivered more rapidly than those in the songs of *S. texensis* or *S. curvicauda*. The number of pulses per phrase is practically impossible to count except on cool nights. As shown above, it varied from 7 to 9 in the recorded phrases, in which at 73° F. the pulse rate was about 22 per second.

The following authors have described the song of this species:

Cantrall (1943, 6, George Reserve, Michigan)
Pierce (1948, 26, Franklin, New Hampshire)
Walker (1904, 6, Ontario, Canada)
Piers (1917, 6, Nova Scotia).

These descriptions differ from that given above chiefly in that up to 11 pulses per phrase may occur (Pierce), and the speed of delivery of pulses is indicated as somewhat slower than observed in this study (5 per second, Walker). This difference could easily be due to temperature, however, and probably is, since Walker states that the "night" song is more rapid in the afternoon than it is late at night.

Most of the above authors describe the day song (which has not been heard in this study) as a single lisp or pulse, produced at intervals of several seconds.

<u>Scudderia</u> <u>curvicauda</u> <u>curvicauda</u> (DeGeer)

The Curve-Tailed Bush Katydid

<u>Distribution</u>

This species is also northern, with its southern limits rather poorly defined. Rehn and Hebard (1914a, 26) state that it intergrades with <u>S.</u> <u>curvicauda</u> <u>laticauda</u> Brunner in the latitude of southern Kentucky. In the present study it has been observed in central and northern Ohio and northern Illinois between early July and late September, usually near marshy areas, though frequently in well-drained grassy-herbaceous fields, such as clover and alfalfa fields, gardens, and weedy areas of various kinds. Cantrall (1943, 6) found adults between July 13 and September 21 on the George Reserve, Michigan, characteristic of both semipermanent and permanent marshes, erratic in both sunny and shady oak-hickory, and sporadic in bog environments. Blatchley (1920, 6) found adults as early as July 10 in Indiana, and records the species as abundant in marshy meadows bordering lakes and tamarack swamps in northern Indiana. Fox (1917, 6) found adults between July 9 and 14 in bushes and "briery thickets" in the vicinity of woodland in Virginia. Hubbell (1922, 6, Michigan) found adults between July 29 and September 2 in sparse growth of dry grass and low bushes overrun with dewberry vines, sandy fields of dry, sparse grass, and in a bush in a lizard's tail marsh. Hebard (1938, 6, Pennsylvania) says adults appear in early July low in oak trees or on oak sprouts in dry fields and woodlands. He states that this insect is often confused with texensis and the majority of records from marshes are probably based on material of that species.

Singing Behavior

This species has been heard only at night and in late afternoon in the present study, though Cantrall (1943, 6), Rehn & Hebard (1914a, 6), and others report a day song like that of other *Scudderia*. No particularly dense colony has ever been observed; singing males have not been found closer together than 6-8 feet. Singing males perch more or less horizontally, 2-6 feet above the ground, depending on the height of the tallest herbaceous vegetation in the area. Songs are produced at wide intervals and singing by one male is generally quickly followed by song from one or more neighboring males. Males have been observed to stay on one perch for over an hour. A disturbed male flew three times in about an hour, a few yards each time, and sang from each of the perches upon which he alighted between flights.

Song Records

*Franklin Co., O. (University Woods) 8 Aug 1954, 85° F., 24 sec., 8 phrases; 7, 2-pulse; 1, 3-pulse, at intervals; 0-4 - 8.5 - 13.6 - 19 sec., break, then at 0 - 4 - 8.5 sec. (3 songs). Pulse rate, 4.5 per second.

DuPage Co., Ill., 18 Aug 1954, Champaign Co., O., 24 Aug 1954, Williams Co., O., 19 Aug 1954.

Song Description and Analysis

This song is a succession of 2-, 3-, or 4-pulse rasping phrases repeated at fairly regular intervals 3-7 times about 4-6 seconds apart. The first phrase almost invariably contains but one pulse, the second 2 pulses, and the rest 2 or 3 pulses. Rarely 4-, 5-, and 6-pulse phrases are heard. The interval between each of these series of phrases, which could be said to be the "song" of this species, is usually several seconds, often a minute or more. The pulse rate is 4-5 per second at 85° F.

The song of this species has been described by the following authors:

Rehn and Hebard (1914a, 26, Pine Barrens, New Jersey).
Scudder (1869, 6, New England).
Fulton (1932, 6, North Carolina).
Walker (1904, 6, Ontario, Canada).
McNeill (1891, 6, Moline, Illinois).
Cantrall (1943, 6, George Reserve, Michigan).
Pierce (1948, 6, Franklin, New Hampshire).

All of these authors describe a day song consisting of a single lisp or pulse repeated at more or less irregular intervals. Descriptions of the night song are like that given here, though Cantrall states, "The entire song [2 phrases in his description] is sounded in about ½ second." My observations indicate that in 2-phrase songs, the entire song requires from 3-6 seconds. The difference lies in the length of time required between the two phrases — Cantrall describes this as twice as long as the time between the individual pulses of the second phrase. In the Ohio and Illinois specimens this interval was usually between 4 and 6 seconds.

Fulton's (1951, 6) description of the song of specimens that he believes to be more like laticauda is, "...a single short rasping note, or a rapid repetition of this note, three or four times." This description appears to be almost identical to that given above for curvicauda.

Scudderia texensis Saussure and Pictet

The Texas Bush Katydid

Distribution

Rehn and Hebard (1914a, 26) state that this species occurs from Maine to extreme southern Florida and west to Montana, Wyoming, Kansas, and Texas. In the present study it has been heard and collected in central and northern Ohio and Illinois, between August 13 and August 30. It is apparently most common in marshes or wet areas, though not limited to such locations. In Franklin County, Ohio, it has been found in well-drained alfalfa and clover fields, pastures, gardens, and weedy areas.

Rehn and Hebard (1914a, 26) say this species is almost invariably found in or near marsh, swamp, or bog. Fox (1917, 6) found adults between July 17 and October 3 in areas of tall grasses (Andropogon) and bushes in open fields, pastures, and meadows, and on tall reeds (Spartina cynosuroides) in tidal marshes in Virginia. Blatchley (1920, 6) found the first adults in Indiana on July 22, and says the species occurs on tall, coarse grasses and sedges along lake and pond borders, and in damp ravines, and on coarse weeds along the margins of prairies and meadows. Hubbell (1922, 6) found adults in Michigan from September 4-8 on tall herbaceous plants and bushes along road-sides and in a moist meadow pasture, and on tall plants in cultivated fields, tall grass in a dry bluegrass pasture, among the tall grass and sedge clumps in a ravine sedge marsh, and among the bunch grass on vetch and grapevines in dunes. Hebard (1938, 6) says adults appear in early July in Pennsylvania, and prefer tall weeds and grasses in moist or wet spots, swamps and marshes.

Singing Behavior

This species has been heard only in late afternoon and night in the present study, apparently producing what other authors refer to as the "night song." In Piatt County, Illinois, on 29 August 1954, this species began singing the night song about 3:30 P. M. on a clear, sunny, but cool afternoon. No songs of any kind had been heard the preceding hour while collecting in this field.

Singing males perch on the highest herbaceous vegetation in the area, in a more or less horizontal position, and seemingly are stimulated to song by the starting of song by neighboring individuals.

Song Records

*DuPage Co., Ill. (Bemis Woods) 18 Aug 1954 (temperature not recorded) 2 min. 06 sec., 15 phrases, spaced as follows: (in sec.): 0 - 5 - 10 - (break) 0 - 4.5 - 9.5 - 16.5 - 27.5 - 32 - 47 - 56.5 - 62.5 (break) 0 - 6.5. These phrases contained the following number of pulses: 5, 4, 4, 6, 7, 10, 8, 6, 8, 5, 6, 9, 8, 8, 7. Pulse rate, 6.8 per second.

*Franklin Co., O. (University Woods) 23 Aug 1954, 70° F., 1 min., 36 sec., 25 phrases, spaced in seconds as follows: 0 - 2.5 - 6 - 9.5 - 12 - 14.5 - 17 - 20 - 25 - 27.5 - 32.5 - 35 - 39.5 - 42 - 44.5 - 56.5 - 66 - 69.5 - 73 - 76 - 78.5 - 88.5 - 91.5 - 95. These phrases all contained 4 pulses each, and the pulse rate in several phrases averaged 13.2 per second.

*Bourbon Co., Ky., 15 July 1955 (Collected by Walker and recorded in the laboratory), 84° F., 2 min. 19 sec., Phrases spaced as follows: 0 - 3 - 5.5 - 11.5 (break) 0 - 4.5 - 7 - 9.5 - 14.5 - 17 - 22 - 24 - 36.5 - 42.5 - 49 - 52 (break) 0 (break) 0 (break) 0 (break) 0 - 5 (break) 0 (break) 0 (break) 0 (break) 0 (break) 0 (break) 0 - 5.5 (break) 0 (break) 0 (break) 0 (break) 0 - 6 - 11 - 15 - 25 - 34 - 57.5 - 65 - 67.5 - 73.5 - 79.5 - 88 - 107. The phrases contained the following numbers of pulses: 4, 4, 4, 4, 18, 3, 16, 4, 4, 3, 3, 4, 4, 4, 4, 4, 7, 4, 4, 4, 16, 4, 4, 4, 4, 4, 4, 15, 4, 4, 16, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4. Pulse rate 13.6 - 19 per second.

Song Description and Analysis

In the Kentucky specimen recorded above, the pulse rate was slower in the longer pulses and faster in the slow pulses, varying from 13.6 to 19 per second.

In Piatt County, Illinois, this species was heard to produce phrases containing 3-21 pulses.

The song, as shown above, consists of a series of phrases containing a variable number of pulses, but generally more than in the song of <u>curvicauda</u> and less than in the song of <u>pistillata</u>. The usual number of pulses per phrase is 4, but in certain situations the number may be as high as 21. The pulse rate in this species is almost midway between those in the songs of <u>curvicauda</u> and <u>pistillata</u> (Plate XLIII.) The phrases may be repeated rather regularly at intervals of a minute or more. As with other <u>Scudderia</u> the song is lispy and rather soft, but noticeable several yards away.

This song has been described by the following authors:

Cantrall (1943, 6, George Reserve, Michigan)
Fulton (1932, 6, North Carolina)
(Pierce (1948, 6, Franklin, New Hampshire)
Allard (1911a, 6, Oxford, Massachusetts; 1910, 6, Washington,D. C.)
Scudder (1893, 6)
Rehn and Hebard (1914a, 26, New Jersey).

These descriptions are essentially in agreement with that given above, though Cantrall and Scudder describe "day" songs. Cantrall says, "The day song of <u>texensis</u> may be represented by 'zeeck-tseek,' or better yet as 'skee-deeck.' ... complete song lasts three-quarters of a second." Scudder says the day song is a single <u>tzip</u> or <u>bzrwi</u> lasting 1/3 second. Allard describes a song like the night song described above, and another kind of song as, "...a succession of sharp, keen, distinctly rasping notes slowly delivered, zeet-zeet-zeet-zeet...usually by some other individual elsewhere." This

PLATE XLIII. SONGS OF SOME TETTIGONIIDAE

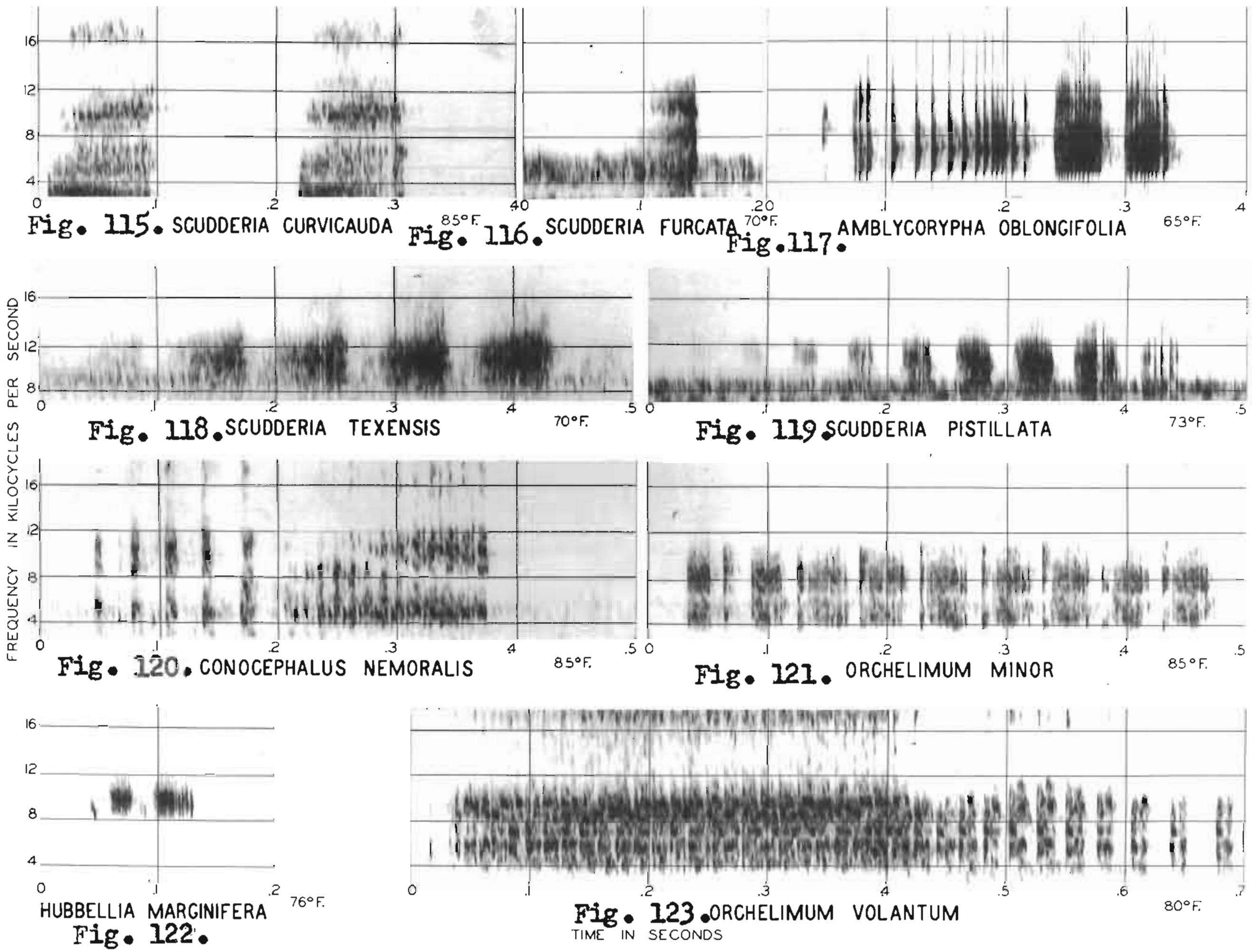


Fig. 115. SCUDDERIA CURVICAUDA 85°F.

Fig. 116. SCUDDERIA FURCATA 70°F.

Fig. 117. AMBLYCORYPHA OBLONGIFOLIA 65°F.

Fig. 118. SCUDDERIA TEXENSIS 70°F.

Fig. 119. SCUDDERIA PISTILLATA 73°F.

Fig. 120. CONOCEPHALUS NEMORALIS 85°F.

Fig. 121. ORCHELIMUM MINOR 85°F.

HUBBELLIA MARGINIFERA 76°F.
Fig. 122.

Fig. 123. ORCHELIMUM VOLANTUM 80°F.

sounds more like *S. curvicauda*; it may have been due to low temperature, or to a difference in the song of this species in Massachusetts.

Scudderia furcata furcata Brunner

The Fork-Tailed Bush Katydid

Distribution

Rehn and Hebard (1914a, 26) state that typical *furcata* is known from Maine to Florida and around the coast to Corpus Christi, Texas, then north to Uvalde and Sweetwater, Texas, Glen, Nebraska, and Hot Springs, South Dakota. They also cite records from Wisconsin, Ontario, and Quebec. In the present study it has been encountered from Hocking County to Williams County in Ohio, and in Piatt and DuPage Counties in Illinois. It occurs in abundance both in the small trees along the border of the ridgetop forests, and in *Andropogon*-dominated hillsides in Hocking County, Ohio, and in marshy areas in Champaign and Williams Counties, Ohio, and DuPage County, Illinois. At Columbus, Ohio, I have heard it only between August 18 and September 21, though its soft lisp could easily be missed in the early part of the season.

Rehn and Hebard (1914a, 26) state that in New Jersey this species matures a month later than S. curvicauda, appearing adult in the pine barrens in mid-August. Hubbell (1922, 6) found adults of this species between August 8 and August 31 in North Dakota, on shrubbery and young trees in the margins of the woods bordering the Cheyenne

River, and at Fargo in shrubbery and tall nettles, and along the margins of an open grove near the banks of the Bois-de-Sioux River. Hubbell (1922, 6) found adults in Michigan from June 26 to September 9 in dry fields of second growth scrub, bushes and tall weeds in woods margins, low herbaceous vegetation in an open oak forest, in the lower limbs of trees in the forest margin, along roadsides, and in orchards, among tall grass in dry fields and pastures, and in the dune area, from the grassy ridges along the side rims of blowouts and on vines growing among the bunch grass. Hebard (1938, 6) says adults appear in early August in Pennsylvania, and are found in tall herbage and in bushes and trees of both dry and wet areas. Cantrall (1943, 6) says this species is characteristic of both the permanent and the semi-permanent marsh habitats on the George Reserve, Michigan, but is most abundant in the latter. "In late August, when the species is most numerous, individuals tend to wander. At this time erratics have been noted in the mixed grass-herbaceous habitat and in the low shrub-terrestrial stratum of both the sunny and the shady oak-hickory habitats, but never more than fifty yards from the nearest characteristic hydric environments. Sporadic groups occur in the bog habitat." He says adults can be found from late July until frost. Morse (1920, 6) found adults from July 26 to October 10 in tall grasses, bushes, clumps of bayberry and huckleberry. Blatchley (1920, 6) records adults as appearing about July 15 and he found nymphs in Vigo County, Indiana, as late as September 15.

The above differences in the description of the habitat of this species are of some interest and deserve further investigation. Similar difficulty in describing habitat is encountered in other species, such as Amblycorypha rotundifolia, with different investigators stating categorically that the species inhabits "wet" or poorly-drained areas, while others are sure that this species can be found only in "dry" or well-drained areas. In Hocking County, Ohio, this species occurs in such great numbers on high, dry ridgetops and hillsides, that the individuals cannot possibly be described as "waifs" or "wanderers." On the other hand, it occurred almost as abundantly around the edges of a large marsh in DuPage County, Illinois. Significantly, A. rotundifolia occurred in both areas also. Apparently the wrong factors are being used to delimit or describe the habitats of these species.

Singing Behavior

This species has been heard both day and night, and the song apparently is the same. Allard (1911a, 6) and Cantrall (1943, 6) state that it sings more often during the afternoon than at night. My own observations have not been sufficient to substantiate or disprove this suggestion. Singing males are usually located from 2-8 feet above the ground, perched horizontally. On a few occasions individuals have been heard and spotted in trees, as much as 20 feet above the ground.

Song Description and Analysis

Only one rather poor recording was obtained of this species, about 20 seconds containing 3 single-pulse lisps, on 18 August 1954 in Bemis Woods, DuPage County, Illinois (Plate XLIII). The song is not particularly loud or noticeable, and is easily missed, especially at night. On one occasion, at Ash Cave in Hocking County, Ohio, a few double- and triple-pulse phrases were heard from an individual spotted singing from a tree.

The song of this species has been described by the following authors:

Cantrall (1943, 6, George Reserve, Michigan)
Riley (1874, 6, Missouri)
Snodgrass (1923, 6, Washington, D. C.)
Fulton (1932, 6, North Carolina; 1930, 6, Oregon)
Pierce (1948, 26, Franklin, New Hampshire
Allard (1910d, 6, Thompson's Mills, Georgia; 1911a, 6, Oxford, Massachusetts)
Walker (1904, 6, Ontario, Canada).

In general all these descriptions agree with that given above. However, Cantrall only heard single-pulse phrases, while Fulton describes 1-4-pulse phrases, Riley, 1-3-pulse phrases, Pierce, 2-pulse phrases, and Allard, 1-3-pulse phrases. Walker describes the song simply as "very like that of pistillata," which is difficult to explain.

Cantrall, Pierce, and Fulton also describe a soft, ticking song which has apparently not been noted by the other authors, and which I have never heard. Riley states that the song of the male is occasion-responded to by a faint chirp from the females, produced by stretching out their wings, as if for flight.

Fulton (1930, 6) heard the ticking in Oregon, and describes it as usually repeated several times in series, but with the frequency varying from 2 to 3 seconds apart to a rate too rapid to count. He also describes a third sound which is "like the single note rapidly repeated 3 or 4 times as if the tegmina were vibrated, while bringing them together."

Cantrall describes the ticking as a "...series of slow lispings which sounded like 'tsips.' These were only a fraction of a second in length and were given every 2 and one-half seconds. The notes were barely audible five feet away." He heard this song but once. Pierce described the ticking as "...a large number of very short pulses (clicks) of duration about .01 sec., and separated by intervals which average about .18 second."

The relationship of these three sounds to each other is unknown. It may represent behavior similar to that of Microcentrum rhombifolium, which produces two entirely different songs for which the difference in stimulus is unknown.

Scudderia fasciata Beutenmuller

The Hemlock Bush Katydid

Distribution

This species was described by Beutenmuller from West Woodstock, Connecticut, and was treated as a synonym of S. furcata Brunner by Rehn and Hebard (1914a, 26) and subsequently by Blatchley (1920, 6) and others, until Dr. E. S. Thomas pointed out to Hebard (1938, 6) that the two were quite distinct in Ohio. Hebard said that the adults appear in August and it prefers hemlock and other northern conifers. In the present study this species has been observed and collected on only three occasions, twice during the day and once at night, in Goodhope Township and at Ash Cave in Hocking County, Ohio, between September 11 and 14, 1954. At Ash Cave, fasciata and furcata occur together in the hemlock-deciduous forest at the head of a ravine.

Singing Behavior

This species is scarcely ever found less than 8 or 10 feet above the ground, in my experience only in hemlock trees. It is so difficult to locate by its song that no suitable recordings were obtained during one whole evening spent in the forest at Ash Cave where its soft lisps literally filled the air. Songs were heard during the day at Ash Cave, but it apparently sings in much greater numbers by night. No singing individuals were ever spotted; the few collected were obtained by sweeping the lower branches of the hemlock trees.

Song Description and Analysis

The single recording made at Ash Cave at 65° F. is 42 seconds long and contains 5 soft, single-pulse lisps by 2 individuals, 2 pairs at 3.5 and 2-second intervals, and a single lisp by one individual 30 seconds from the others. Both 2- and 3-pulse phrases were also heard, and this song is thus far inseparable from that of S. furcata.

Amblycorypha oblongifolia (DeGeer)

The Oblong-Winged Katydid

Distribution

The limits of distribution of this species are uncertain, due to the fact that Rehn and Hebard (1905, 26) described a new species, A. floridana floridana, then later (1914a, 26) a subspecies, A. floridana carinata, which Blatchley (1920, 6) recognised as a subspecies, and about which Fulton (1932, 6, 1951, 6) is uncertain. However, since all the recordings and observations of the present study were made in Ohio, Indiana, Illinois, and Kentucky the specimens treated can be considered to be typical oblongifolia. Rehn and Hebard give the range of typical oblongifolia as from New Hampshire to North Carolina and west to San Antonio, Texas and Manitou, Colorado. They say that floridana floridana occurs in Florida and Texas, merging in Georgia and South Carolina with floridana carinata, which extends north through Virginia, New Jersey, Pennsylvania, and Massachusetts. Fulton (1932, 6) records only oblongifolia from North Carolina, and his description of the song fits that described here for this species. In 1951, 6, however, Fulton lists only floridana carinata from Raleigh, stating that a form (with a distinct type of song) occurs along the salt marshes on the North Carolina coast "...which may be typical *floridana*."

This species occurs in a variety of situations in Ohio, Indiana, and Illinois, but is especially common in marshy or poorly drained areas, along the border of swamp forest associations, and in brushy or vine-filled fencerows. At Columbus, Ohio, its song is heard from mid-July until heavy frost. The most dense colony ever encountered was in a patch of giant ragweed (*Ambrosia trifida*) under a cottonwood tree along a recently mowed river bottom oats field. Here both males and females could be found on almost every plant, sometimes only a foot or so apart.

Blatchley (1920, 6) records adults "about July 20" in southern Indiana, and says this species occurs on shrubbery and flowers of golden-rod and other Compositae along fencerows and edges of thickets and woods, especially in damp localities. Hubbell (1922, 6) found adults from July 16 to September 4 in Michigan, common in sedge and lizard's tail marshes, low forest margin thickets, roadside thickets of tall weeds and bushes, clumps of shrubbery in fields and pastures and about the margins of open woods, and in tall rank weeds and shrubs around lake margins. Hebard (1938, 6) says adults appear in July in Pennsylvania, and are found in rank weeds and vines, particularly in moist areas at the forest edges. Cantrall (1943, 6) found adults from mid-August to late September in permanent and semi-permanent marsh habitats on the George Reserve, Michigan.

Singing Behavior

The calling song is produced at night only, having been heard in the present study as late as 3:30 A. M. As shown in Plate XIX, it begins rather late in the evening, after most of the other night-singing species in the same areas have already started. However, Walker (1904, 6) states he heard it "...at night and in the afternoon when the sun was shining..." in Ontario. The lowest temperature at which this species has been heard singing is 55° F.

Different individuals alternate their chirps, the beginning of song by one individual apparently stimulating his neighbors. The individuals in a colony usually sing a few minutes, alternating chirps with one or two other individuals, then are silent for a few minutes before starting up again. Colonies thus sing in bursts, separated by intervals in which no individuals are singing.

Males caged in close proximity in the laboratory produce a sound distinct from the calling song, and Blatchley (1920, 6) states that "...on several occasions it [the song] has been made after the insect was in my fingers." I was unsuccessful in several attempts to get captured males to produce such a "protest" sound. Apparently the only other North American orthopteran in which sound production has been noted by an individual captured or disturbed (prodded, squeezed, held, or shaken) is *Pterophylla camellifolia* (Fabricius).

Song Records

The calling song of this species has been heard practically continuously throughout its singing season around Columbus, Ohio.

*Franklin Co., O. (Clinton Twp.) (1) 28 Jul 54, 75° F., 16 chirps/44.5 sec. (2) 8 chirps/18 sec. (3) 21 chirps/50 sec. (4) 19 July 1955, 6 chirps/25 sec., 79° F.

*Franklin Co., O. (Plain Twp.) 21 July 1955, 80-85° F.,

*Carroll Co., O. (Specht Marsh) 14 Aug 1954, 65° F., (1) 17 chirps/53 sec. (2) 13 chirps/43 sec.

*Erie Co., O. (Cedar Point) 26 July 1955, 78° F., (1) 18 chirps/40 sec. (2) 4 chirps/15 sec. (3) 20 chirps/60 sec.

*Bourbon Co., Ky., 16 July 1955, 84° F.

*Piatt Co., Ill., 5 Sept 1955, 55° F., 20 chirps/89 sec.

Song Description and Analysis

The calling song is a loud, rasping chirp containing 2, 3, or 4 pulses delivered so rapidly as to be run together (Plate XLIII). It lasts about 1/3 second and is repeated with fair regularity every 3 or 4 seconds, usually for several minutes at a time. The first pulse is longer and different from the others in the chirp, giving the impression of speeding up. The chirp ends abruptly, and can best be described as "iz-z-z-zi-zik." It is fairly loud, and noticeable several yards away, even when other insects are singing.

The "fight" sound (produced by males caged together) was noted on several different occasions in two Kentucky males caged together. It consisted of several uniform single-pulse chirps produced several times in succession at a rate of 1 or 2 per second. A similar sound has been heard from males just starting up in the evening outside in Franklin Co., O., but in these cases the single-pulse chirp was produced only once when song was started.

Table 9

Analysis of songs of <u>A. oblongifolia</u> (DeGeer)

Locality	Date	Temp.	No. of Chirps	No. Chirps with 1,2,3, 4 Pulses				No of Ticks be-tween chirps	Average Chirp Interval
				1	2	3	4		
Franklin Co. O.	28 Jul 54	75° F.	16		3	13	0	0	3.1 sec.
Franklin Co. O.	28 Jul 54	75	8		0	7	0	0	2.5
Franklin Co. O.	28 Jul 54	75	21		3	17	1	14	3.7
Franklin Co. O.	21 Jul 55	85		1	2	17	4	2	1.3
Franklin Co. O.	19 Jul 55	79	5	0	0	5	0	0	3.5
Carroll Co. O.	14 Aug 54	70	17	0	3	14	0	6	3.1
Carroll Co. O.	14 Aug 54	70	13	0	0	13	0	13	3.3
Erie Co. O.	26 Jul 55	78	20	0	9	8	3	20	2.8
Erie Co. O.	26 Jul 55	78	24	8	7	7	2	17	2.75
Bourbon Co. Ky.	15 Jul 55	75	10	0	0	10	0	0	2-3
Bourbon Co. Ky.	16 Jul 55	85	11	5	1	2	3	4	2.8
Piatt Co. Ill.	5 Sept 55	55	20	0	7	9	4	2	4.7

The following authors have described the song of this species:

Allard (1910c, 6, Plummer's Island, Maryland; Thompson's Mills, Ga.)
Allard (1928a, 6, Washington D. C.)
Allard (1929a, 6, Southern New England compared to Washington, D. C. and southward.)
Blatchley (1920, 6, Indiana)
Cantrall (1943, 6, Michigan)
Fulton (1932, 6, North Carolina)
Pierce (1948, 26, Franklin, New Hampshire)
Snodgrass (1923, 6, Washington, D. C.)
Walker (1904, 6, Ontario)
Scudder (1893, 6)

Of these descriptions, only those of Blatchley, Snodgrass, and Pierce appear to disagree with the analysis here. Blatchley calls it

"...a creaking squawk...usually but once repeated, though sometimes three times." This sound more like _S. curvicauda_.

Snodgrass describes the song of this species as "...a shrill _shrie-e-e-e-k_, _shrie-e-e-e-k_, repeated about 6 times..."

Pierce's analysis of the song makes it appear that he recorded the sound produced by males in close proximity rather than the calling song. However, his analysis of the file length and number of teeth is also quite different, being about the same as for the non-functional file in Ohio specimens. It is impossible to tell from Pierce's figure whether he measured the functional file or the non-functional one, though on other Tettigoniidae, he apparently measured the functional one; 11 Ohio and Illinois specimens measured had functional files varying from 3.0 to 3.5 mm. in length, and possessing from 66 to 82 teeth. The non-functional file on one Ohio specimen was 2.3 mm. long and had 63-65 teeth. Pierce gives a file length of 2.4 mm. with 65 teeth.

Pierce doesn't say whether his recordings of _oblongifolia_ were made with caged specimens or in the field. His graphs show four-pulse chirps in which each successive pulse and interval is longer than the preceding. The toothstrike rate is about 333 per second, and fairly constant. The number of toothstrikes in one 3-pulse chirp was 2 in the first pulse, 6-7 in the second, and 10 in the third. In the songs of Ohio, Illinois, and Kentucky specimens, the pulse intervals within a chirp and the length of all but the first pulse are fairly constant. The number of teeth struck per pulse varies from 9 to 18, but does not increase in successive pulses, as in Pierce's specimens. The first pulse is usually longer than the others, and the rate of toothstrike in this pulse is slow, accelerating toward its end. The rate of toothstrike in the other pulses is about 333 per second.

Pierce also noted ticks between the third and fourth pulse in some chirps. None of these were recorded in the songs of Ohio, Illinois, and Kentucky specimens, but a tick, involving the striking of 1, 2, or 3 teeth, occasionally occurs between chirps. This did not occur in the songs of Pierce's specimens. The chirps recorded by Pierce varied in length from 2 to 4 pulses, as did those recorded in the present study, but Pierce's specimens required .08-0.19 second to complete a chirp, while the specimens recorded in the present study required 0.28-0.49 second.

It is difficult to say whether the above variations are a result of geographic variation, or are due to Pierce recording his specimens in the laboratory and giving data for the non-functional file. Allard (1929a, 6) states that "...the stridulations...as heard in southern New England have a distinctiveness in delivery and rasp that distinguishes them from the notes of the same species in the Washington region and southward." The systematic analysis by Rehn and Hebard (1914a, 26) of this group, and the subsequent remarks of Blatchley, Fulton, and Allard, cited above, suggest that further study is needed to clarify the relationship of the various forms occurring in eastern United States.

Amblycorypha rotundifolia (Scudder)

The Round-Winged Katydid

Introduction

Amblycorypha rotundifolia rotundifolia is the name presently applied to the round-winged katydid as it occurs from South Carolina, Georgia, and Arkansas northward in eastern United States. Rehn and Hebard (1914a, 26) call a western form from Iowa, Kansas, and Missouri, A. r. iselyi Caudell, and a southwestern form, A. r. parvipennis Stal. Hebard (1945, 6) says that parvipennis is a midwestern species, distinct from rotundifolia. Apparently only one name has been applied to the eastern form. However, as will be domonstrated here, two "song forms," which apparently represent distinct species occur in eastern United States. These are distinguishable at present only by their different songs, and by the fact that one is southern, being known from the sand hills of North Carolina north to southern Fairfield County, Ohio, and the other is northern, known from Michigan south to the southern border of the Appalachian Mountains in North Carolina. These forms have been named the "clicker" and the "rattler," respecrively, because of the nature of their songs. Within their overlap zone of some 200 miles no differences in habitat or in seasonal distribution are apparent. In Bath County, Virginia, Pocohontas County, West Virginia, Hocking County, Ohio, and Fairfield County, Ohio, both kinds of individuals are often found in nearly equal numbers in the same colony, apparently randomly intermixed. Other colonies contain only one form or the other. The songs of these two forms are quite different, and no individuals with intermediate songs have ever been heard.

Two males of each form from Hocking County, Ohio, were marked and caged in a large screen cage in the laboratory. On two separate occasions, the beginning of song by one of the rattlers immediately provoked singing by the other rattler, but neither clicker sang. On one occasion, one of the clickers began to sing, and the other immediately followed suit, with no response from either of the rattlers. None of these individuals ever sang another song than the one they were singing when captured. A mixed colony was observed continuously in Hocking County, Ohio, for over two hours one night, and during this time the same songs continued to come from the same perches, indicating that the individuals did not change their song.

It is my opinion that these two forms represent distinct species. However, further study is necessary to eliminate the unlikely possibility that the song differences are due to a single determiner, and the two forms interbreed. Biological studies of these forms may be unusually difficult since no method for distinguishing the females has yet been determined, and in the only related species which has been reared (A. oblongifolia, Hancock, 1916, 26) the eggs required 2-3 years to hatch.

In addition to the wide variation in descriptions of the song of the round-winged katydid by different authors, apparently caused by the presence of the two forms described above, equally wide variations exist in the description of the ecology of <u>rotundifolia</u>, even within the range of the rattler, the form most frequently encountered in the present study. These variations are not correlated with the two song forms, since these occur together in the same habitats where their ranges overlap. Because of the confusion in this regard, theecological situations in which rattler colonies have been observed during the present study are listed below.

1. Franklin County, Ohio - dry hillside covered with bluegrass, teasel, sweet clover, Queen Anne's lace, and with no trees within 100 yards.

2. Franklin County, Ohio - patch of giant ragweed in the center of a damp forest in a semi-cleared spot. This forest contains old beech and sugar maple trees, but the young trees are elm, soft maple, and white ash, and the forest floor is poorly drained, marshy in some areas.

3. Hocking and Fairfield Counties, Ohio - well-drained hillside pastures, both closely grazed and overgrown with sumac, pine, and dominated by <u>Andropogon virginicus</u>. Here the rattler and the clicker occur together in company with abundant colonies of <u>Scudderia furcata</u>, <u>Atlanticus testaceous</u>, <u>Miogryllus verticalis</u>, <u>Arphia sulphurea</u>, and the prairie <u>Acheta</u>.

4. Adams County, Ohio - along a grassy lane on a forest border, on teasel.

5. Pocohontas County, West Virginia - along the edges of the forest along the highway through the mountains, both near the mountain-

tops, and in the valleys (both rattler and clicker in these locations.)

6. Licking County, Ohio - grassy, weedy, and brush-filled roadsides.

7. DuPage County, Illinois - along the edges of a swamp forest bordering a semi-permanent marsh, in company with Scudderia furcata, Nemobius fasciatus, N. confusus, Orchelimum nigripes, Anaxipha exigua.

8. Carroll County, Ohio - One female collected in a power-line clearing through an oak-hickory forest, in the middle of a colony of Nemobius tinnulus.

9. Hocking County, Ohio - one male heard singing in a small hemlock half-way up an oak-covered ridge.

10. Cuyahoga County, Ohio - in the forest border along the roadside.

11. Franklin County, Ohio - in the edges of the forest along a road through Blendon Woods.

Cantrall (1943, 6) remarks on the contradictory nature of statements in the literature regarding the habitat preferences of this species, and states that on the George Reserve, Michigan, it is "...decidedly characteristic of the shady oak-hickory habitat... occurring ...also in much smaller numbers as a sporadic in the sunny oak-hickory habitat." He regards the report of a single individual supposedly collected in an area of mixed grass-herbaceous upland fully two hundred yards from the nearest patch of woods as possibly due to an error on the part of the collector. The situations listed above indicate that in Ohio, Illinois, Virginia, and West Virginia, although occurring commonly in well-drained areas perhaps comparable to Cantrall's sunny and shady oak-hickory habitats, it is also found in rather dense colonies in poorly-drained situations, and in grassy-herbaceous upland quite isolated from forest of any kind. Such habitats are indicated by Blatchley (1920, 6), Morse (1920, 6), Fox (1917, 6), and Allard (1911a, 6), whose statements are summarized by Cantrall.

This species, like many other of our presently common Orthoptera, is apparently well-suited to come common characteristics perpetuated in our roadsides, pasture fence lines, and other similar situations. A common criticism leveled at the distribution records of some collectors, that the points plotted obviously follow the roads, is probably inappropriate with species such as these, since they actually do occur most abundantly and frequently in roadside associations.

At Columbus, Ohio, the rattler is heard from early July until heavy frost. Hebard (1938, 6) says adults appear in July in Pennsylvania; Fox (1917, 6) found adults between July 30 and September 3 in Virginia; Morse (1920, 6) says it matures in late July or August in New England; Cantrall (1943, 6) found adults between July 18 and September 15 on the George Reserve, Michigan; Fulton (1951, 6) cites records of adults from late June until early October at Raleigh, North Carolina; Blatchley (1920, 6) says the males mature about the fifth of July in southern Indiana, the females about a week later.

Singing Behavior

Like the other two eastern species in this genus, rotundifolia perches horizontally while singing, usually 2-3 feet above the ground, and sings at night only. Both in the field and in the laboratory, the starting of song by one individual causes his neighbors to start up also. Individuals do not alternate any of the elements of their songs, as with oblongifolia, or synchronize them as with brachyptera (Fulton, 1930, 6), or parvipennis, but begin singing in a sort of "chain reaction," so that their songs overlap. Colonies sing in bursts, separated by silent intervals in which there are no individuals singing.

Song Records

Rattler

*DuPage Co., Ill. (Bemis Woods) 18 Aug 1954, 70° F., 1 min. 22 sec., 3 songs, containing 3,8, and 10 phrases each.

*Hocking Co., O. (Ash Cave) 11 Sept 1954, temperature around 65° F., 4 min. 20 sec., 15 songs containing 2-8 phrases each.

*Adams Co., O. (Jefferson Twp.) 9 July 54 (1) 60° F., 42 sec., 20 short phrases (2) 85° F., 4 individuals caged together 5 min. 43 sec., 9 songs containing 18-74 phrases each.

*Fairfield Co., O. (Goodhope Twp.) 12 July 1955, 69° F., (1) 85 sec., 5 songs, 33 phrases, (2) 100 sec., 2 songs and a part of 3rd, 21 phrases, (3) 84° F., 64 sec., 2 individuals singing together.

*Erie Co., O., 26 July 1955, 76° F., 1 min., 40 sec., 10 songs, containing 2-9 phrases each.

Dickenson Co., Va., 6 Aug. 1955; Bath Co., Va., 11 Aug. 1955; Pocohontas Co., W. Va., 11 Aug. 1955; Licking Co., O., 17 July 1955; Carroll Co., O., 14 Aug. 1954.

Clicker

*Hocking Co., O (Neotoma) 3 Sept 1954, 65° F., 48 sec., parts of 3 songs.

*Fairfield Co., O. (Goodhope Twp.) 12 July 1955, about 65° F., (1) 5 min. 8 sec., 13 songs containing 6-39 phrases each, lasting 5-24 sec. and separated by intervals of 4-13 sec. (2) 6 min., 19 songs containing 1-34 phrases each, lasting up to 19 sec., and separated by intervals of 5-24 sec. (3) 83° F. (lab), 3 min. 8 sec., 15 songs containing 20-24 phrases each, lasting 5-7 sec. each, and at intervals of 4-17 sec.

*Bath Co., Va., 11 Aug 1955, 75° F., 1 min. 26 sec., 4 songs, containing 26, 31, 34, 34 phrases and separated by intervals of 7, 10, 11 seconds.

Blowing Rock, N. C., 7 Aug 1955.

Song Description and Analysis

The song of the rattler or northern song form is composed of from 2 to 3 to a dozen or more phrases in undisturbed singing, each consisting of a group of pulses (Plate XLIV). The song lasts from 2 to 4 seconds on warm nights (80° F. plus), and as long as 10 or 15 seconds when the temperature is around 60° F. The phrases or pulse groups are of unequal length; the first ones in a song are usually short, containing 5 to 25 pulses, and successive phrases increase slightly in length. Finally a long phrase containing 100-200 or more pulses is produced, which is then usually followed by 2 or 3 very short phrases containing only 4 or 5 pulses each. The individual pulses are produced at rates varying from 16 to 25 between 60° F. and 80° F. Each pulse contains about 6 toothstrikes. The breaks between phrases or buzzes in a song last about 1/5 second, and the

PLATE XLIV. AMBLYCORYPHA ROTUNDIFOLIA

Fig. 124. RATTLER

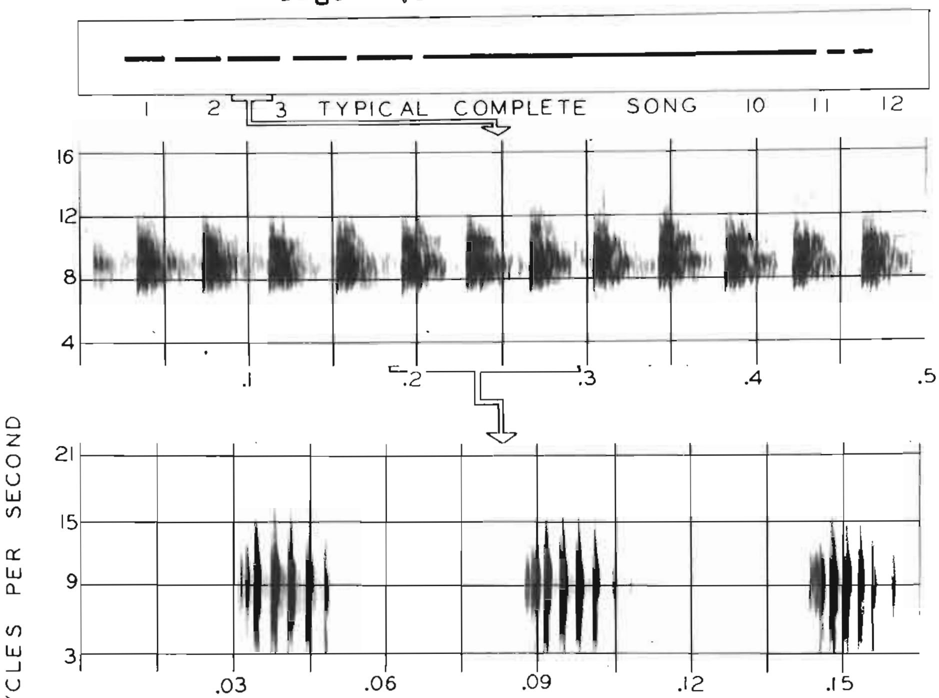
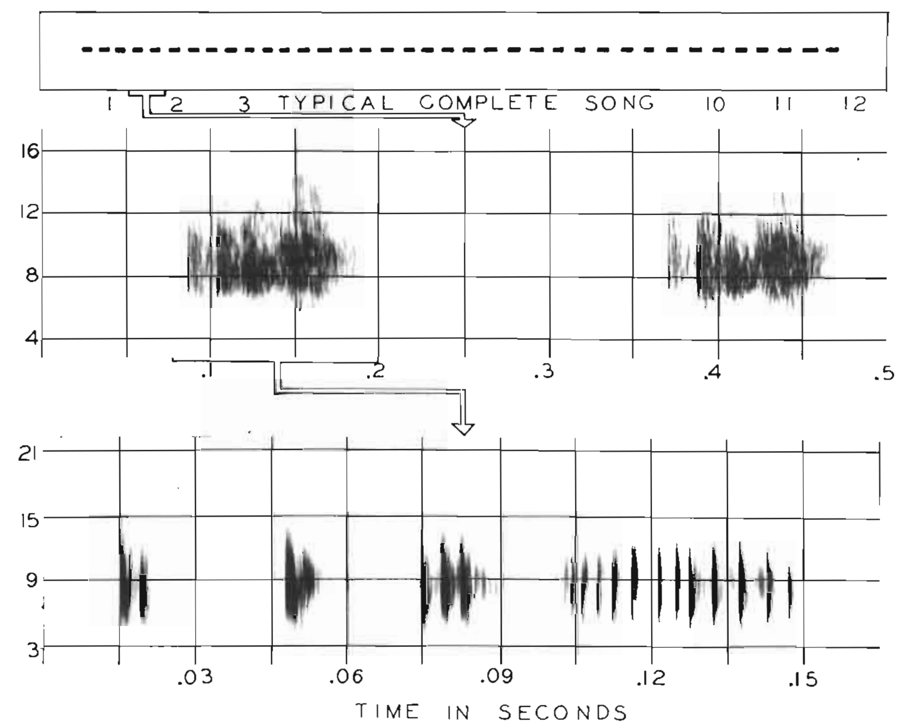


Fig. 125. CLICKER



song interval is variable, from 5 or 10 seconds to a minute or more. Usually several songs are produced at short intervals, then a long interval occurs before further singing. Disturbed individuals shorten their phrases and produce either very short or very long songs.

The song of the clicker or southern form consists of a repetition of from 16 to 39 phrases (normal singing), each of which contains 1-5 pulses (Plate XLIV). The rate of production of these phrases increases slightly toward the end of the song, varying from 3 to 5 at 80° F. The pulses within each phrase are not uniform, the first 1 or 2 involving only 2 or 3 tooth strikes, the next usually having 1-2 more toothstrikes, and the last containing 10-15 toothstrikes. Disturbed individuals shorten their songs and increase the length of the song interval.

As can be seen in Plate XLIV, there is no relationship between these two songs except that the structure of the individual tooth-strikes and their rate of production are alike. Above this level the rhythms are not even remotely similar, a surprising degree of difference for two such closely related species.

The two song forms described above have been noted by earlier authors. Fulton described both songs from North Carolina, stating that the rattling form was heard in the mountains and the clicking form in the sand hills. Allard (1911a, 6, 1912a, 6) gave two conflicting accounts of the song of rotundifolia, as was noted by Cantrall. In 1911, he describes the song, heard at Oxford, Massachusetts, in the following manner: "Its notes are soft and lisping and continue indefinitely. They may be expressed thus: 'tsip-i-tsip-i-tsip-i-tsip.'" This could well be the clicking song though the locality seems peculiar in view of the apparent southern distribution of this form. In 1912, Allard states, "The stridulations of Amblycorypha rotundifolia may consist of brief, soft shuffling phrases, 'sh-sh-sh-sh,' repeated at intervals." This is obviously the rattling song, and the apparent contradiction led Cantrall to suggest that Allard's earlier observation may have been based on too few observations. However, Cantrall failed to note Allard's next statement, "At other times the notes become more lisping and continuous, 'tsip-i-tsip-i-tsip-i-tsip.' The different call notes of this katydid are very similar to those of the smaller katydid, A. uhleri." It is possible that Allard heard both the clicking song and the rattling song, or that he heard only the rattling song, but heard it on a warm night and on a very cool night. The pulse rate in this song is such that the difference caused by this change in temperature causes the song to sound entirely different to the human ear.

Scudder (1893, 6) describes the song as consisting of "...from 2 to 4 notes - sounding like 'chica-chic' - repeated rapidly so as to almost be confounded, and when three requiring just 1/3 of a second; the song is repeated at will, generally once in about 5 seconds, for an indefinite length of time." This sounds like the clicking song, though both the rate (one phrase every 5 seconds) and the "for an indefinite length of time" are at odds with the clicking song as heard by this writer. This discrepency may have been due to his having heard it on a very cold night.

Amblycorypha uhleri Stal

Uhler's Katydid

Distribution

This small katydid is southern in distribution, extending only to the Fairfield-Hocking County line in central Ohio. Rehn and Hebard (1914a, 26) say it occurs from southern New Jersey to southern Florida, and west to central Illinois, Minnesota, and on to Oklahoma and south in Texas to Victoria. In 1934, 26, however, Hebard notes that the Minnesota record is an error. Blatchley (1920, 6) says that this species reaches approximately to the same point, somewhere near the border of unglaciated territory, as the prairie *Acheta*, the clicker *A. rotundifolia*, *Miogryllus verticalis*, the fast tinkling *Anaxipha*, *Oecanthus pini*, and *Orchelimum minor*. The last two species named are obviously limited by the distribution of pine; the other five species all occur in the *Andropogon*-covered, abandoned fields on the hillsides in southern Ohio, which in the course of time eventually become overgrown with sumac and pine, and finally oak forest. The close ecological relationship of these seven species, and its relationship to their northern limits in Ohio is evident.

This species occurs commonly along roadsides in southern Ohio, in addition to the situation already described, and along forest borders near the ridgetops. At Raleigh, North Carolina, it was abundant in a stubble field, and in grass and weeds along a forest border. In

Ohio it has been heard only on a few occasions in September during the present study.

Fulton (1932, 6, 1951, 6) says adults of this species occurs in North Carolina between mid-July and November 7, and are found on tall weeds and bushes. Fox (1917, 6) found adults between July 31 and October 8 in Virginia, in trees, bushes, weeds, and tall grasses of fields, pastures, and roadsides, chiefly in open country. Blatchley (1920, 6) says this species frequents the tall sedges and willows bordering the large ponds in the Wabash River bottoms in southern Indiana. He also took it on and beneath black and scarlet oak, saying that the young sometimes feed on the leaves. Blatchley's observations of the habitat seems a little at variance with those of the present study and other authors. Hebard (1934, 26) cites records for this species from July 27 to September 2 in Illinois.

Singing Behavior

This species sings at night only, and the singing males perch horizontally on herbaceous vegetation, usually about 3 feet above the ground. Singing is not steady for long periods of time, but as with the other Amblycorypha discussed here, and the Atlanticus, there are often gaps of several minutes between bursts of song by the individuals in a colony. Usually after a male starts his song, one or more other individuals join in quickly, and each repeats the entire song several times, then dropping out one by one until all are again silent. Singing males are generally several feet apart and several individuals observed continuously for about 2 hours on one occasion remained on the same perches during that time.

Song Records

*Hocking Co., O. (Neotoma) 3 Sept 1954, 65° F., 53 sec., 2 songs in 1 min. 57 sec.

*Raleigh, N. C. (McCuller's Pond) 8 Aug 1955, 75° F., 9 songs in 6 min. 26 sec.

Song Description and Analysis

The calling song of Uhler's katydid is a soft sound, audible only a few yards away, and is probably the most complicated sequence of sounds produced by any American orthopteran. It lasts up to 40 or 50 seconds, and contains 3 or 4 distinct phases which are consistently repeated in the same sequence in every song. A typical song is diagrammed on Plate XLV, and Vibragrams of the individual pulses in each phase are shown. The range of variations indicated is for the 9 songs of the Raleigh specimen. The song begins with a rapid, tsip-i-tsip-i-tsip-i-tsip which continues for about 7-11 seconds, and involves pulses delivered at a rate of about 12 per second (probably 6 wingstrokes). This merges abruptly into a slower delivery of about 7 pulses per second which lasts only about 2 seconds, and ends with an abruptly louder rattly phrase which dies away in intensity. This phrase, which contains 7 or 8 pulses delivered at a rate of about 10 per second, slowing at the end, is repeated anywhere from 3 or 4 to 10 times at intervals of 1/2 to 6 3/4 seconds

PLATE XLV. THE CALLING SONG OF AMBLYCORYPHA UHLERI

DIAGRAM OF A TYPICAL COMPLETE SONG
AND
VIBRAGRAMS OF PORTIONS OF EACH PHASE

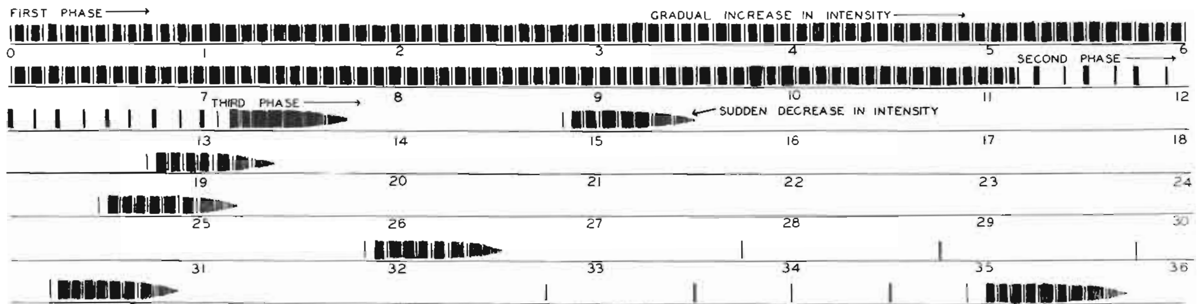


Fig. 126.

Fig. 127. LAST PART OF FIRST PHASE (95-143 WINGSTROKES IN COMPLETE SONG)

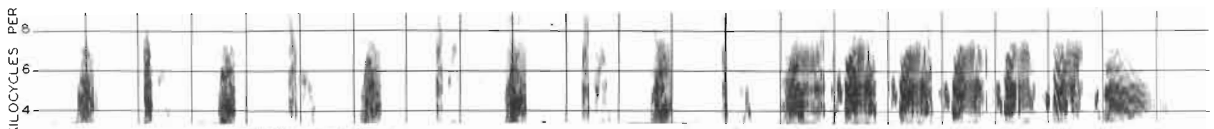


Fig. 128. SECOND PHASE (8-10 WINGSTROKES PER SONG)

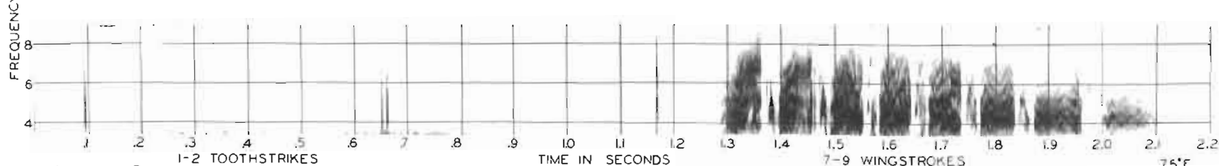


Fig. 129. TICKS (1-14 BEFORE EACH RATTLE) RATTLES (5-10 AT 1/2-11 1/2 SECOND INTERVALS)

THIRD PHASE

(in the songs recorded). Often one or more of these phrases is preceded by a few soft ticks, apparently caused by striking individual file teeth. At least 4 different kinds of pulses are involved in the 3 different phases of this song, and there are both gradual and abrupt changes in intensity, and in speed of wing motion.

This is an amazingly complex pattern for an insect song, and it is a point of interest that no other North American species has a song even approaching it in complexity. Oddly enough, there is apparently very little variation between the song of uhleri in Ohio and several hundred miles south in North Carolina, while other species with much simpler songs often vary a great deal across this range. It is difficult to explain the development and maintenance of such complexity and uniformity unless each of the major phases of the song have a special significance for either the males or the females, or both. Such discrimination would, however, be in marked contrast to the generalisations made by Busnel et al. concerning the discriminatory capacity of insects as far as their own sounds are concerned (see p. 18).

The song of this species has been described by the following authors:

Allard (1910c, 6, Washington, D. C. and Thompson's Mills, Georgia.)
Fulton (1932, 6, North Carolina)

Both author's descriptions agree with that given here. Allard states that there may be variation as to which phrases are used in a particular song, and if two males are stridulating near each other the response is likely to be similar.

Microcentrum rhombifolium (Saussure)

The Broad-Winged Katydid

Distribution

This species apparently occurs throughout the area studied. Blatchley (1920, 6) says that it extends from N. Y. to Florida, west to Michigan, Minnesota, Nebraska, Oklahoma, Texas, Arizona, and Claremont, California, though he says that it has not been noted north of Lafayette, Indiana. Hebard (1934, 26) records it from Twin Grove in north-central Illinois, and states that it undoubtedly occurs throughout the state, as it is known as far north as Lansing, Michigan, and Winona, Minnesota (Lugger, 1897, 26). He believes that rhombifolium was very scarce throughout northern Illinois. In the present study this species was abundant in DuPage County, Illinois, and in northwestern Williams County, Ohio. Cantrall does not list this species from the George Reserve, Michigan.

At Columbus, Ohio, this katydid sings from mid-July until frost, though its numbers seem to fall off greatly past mid-September. It is generally found in trees, both in town and in heavy forest, usually 20-30 feet above the ground. However, on several occasions, considerable numbers of males have been heard singing from bushes and small trees, within 4-5 feet of the ground. Hebard cites records of adults from August 10 to October 20 in Illinois; Fox (1915, 6) says it is heard continuously throughout late July and August at Lafayette, Indiana; Hebard (1938, 6) says adults appear in late July in Pennsylvania, and are arboreal, sometimes present in bushes or in forest undergrowth. Fulton (1932, 6) found adults at Raleigh, N. C., from mid-July to mid-September.

Singing Behavior

The singing behavior of this species is unique for two reasons. First, the males produce two very distinct songs, for which the difference in stimulus situation has not yet been defined, and second, though this species is a night-singer, beginning in large numbers at dusk, one or a few individuals are frequently heard singing at midday on the brightest, hottest days of the summer, and at all other times of day. Other night-singing Tettigoniidae often burst into song after a shower of rain, or on dark, cloudy days, possibly influenced by the drop in temperature, rise in humidity, or drop in light intensity associated with such an event, or by some combination of these factors. But in these cases the whole colony sings; with rhombifolium single individuals in a colony keep singing during the day. Likewise rhombifolium does not seem to start singing any earlier in the evening than the other night-singers, as would be expected if this were a simple matter of the inhibitory influences of light intensity and/or the stimulatory effects of the drops in temperature and/or rise in humidity which generally occur in the evening affecting this species at a slightly different level than other "night singers."

The two different songs produced by males of this species may be associated with the observations made by Fulton (1933, 6), who found that the males of this species go to the females, rather than vice versa, apparently attracted by a soft sound made by the female. However, no observations have been made to connect either of the two songs of the males with a specific situation. I have noted that all the males in an area are usually singing the same song at the same time, and that if the same area is visited a few hours later, they may be singing the other song. A single individual may alternate back and forth from one song to the other several times in one night. One male brought into the laboratory sang only one kind of song (lisping) in the laboratory, though he was captured while singing the other song (ticking) in the field. Fulton (1933, 6) is apparently the only person to ever actually watch a male switch from one song to the other, although Allard described both songs for this species in 1928.

The males perch more or less horizontally while singing, as with other Phaneropterinae, and seem fairly sedentary under certain conditions. This would indicate that an individual male may sing from one spot until he hears a female in the area.

Song Records

Both songs of this species were heard practically every night during its song period at Columbus.

Lisping Song

*Franklin Co., O. (University Woods) (1) 25 Sept 1954, 74° F., 46 lisps in 2 min. (2) 21 Sept 1954, 65° F., 11 lisps in 2 min. 2 sec. (3) 6 Aug 1954, 63° F., 27 lisps in 60 sec.

*Franklin Co., O. (OSU Campus) (1) 3 Aug 1954, 9 lisps in 69 sec. (2) 23 Aug 1954, 9 lisps in 19 sec.

*DuPage Co., Ill. (Bemis Woods) 18 Aug 1954, 14 lisps in 35 sec.

Ticking Song

*Franklin Co., O. (Clinton Twp.) 23 Aug 1954, 71° F., 6 songs in 1 min. 45 sec.

*Franklin Co., O. (Borror) 14 Sept 1954 (1) 4 songs in 52 sec., (2) 9 songs in 32 sec., (3) 9 songs in 35 sec.

*Piatt Co., Ill. (Sangamon Twp.) 5 Sept 1955, 60-70° F., 5 songs in 1 min. 19 sec.

Both Songs Heard

Licking Co., O. (Buckeye Lake) 15 Sept 1954; Pickaway Co., O. (Pickaway Twp.), 10-11 Sept 1954; Hocking Co., O. (Neotoma) 3 Sept 1954, 14 Sept, 1954; Hocking Co., O. (Ash Cave) 11 Sept 1954; Williams Co., O., 19 Aug 1954; DuPage Co., Ill. (Hinsdale) 9 Sept 1955; Piatt Co., Ill., 4 Sept 1955., 29 Aug 1955; Raleigh, N. C., 8 Aug 1955.

Song Description and Analysis

The two songs of this species are illustrated on Plate XLVI. The first of these is a single lisp repeated at intervals of 3-5 seconds for an indeterminate length of time. Rarely, a single lisp is heard. Each lisp is produced by a "complete" wingstroke and thus contains many individually indiscernible toothstrikes. The second song is also

PLATE XLVI. THE SONGS OF MICROCENTRUM

MICROCENTRUM RETINERVE

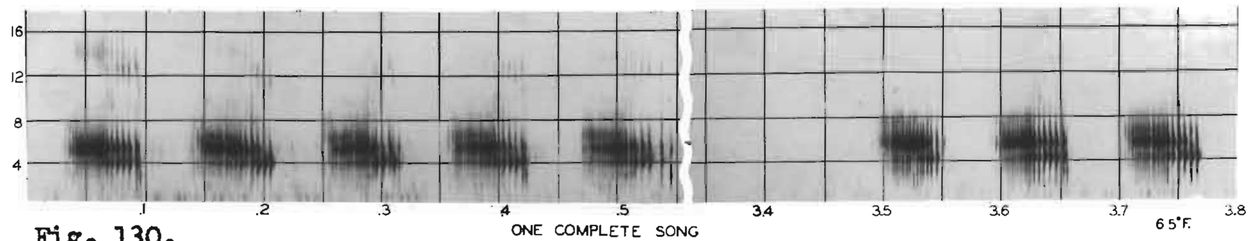


Fig. 130.

MICROCENTRUM RHOMBIFOLIUM

LISPING SONG

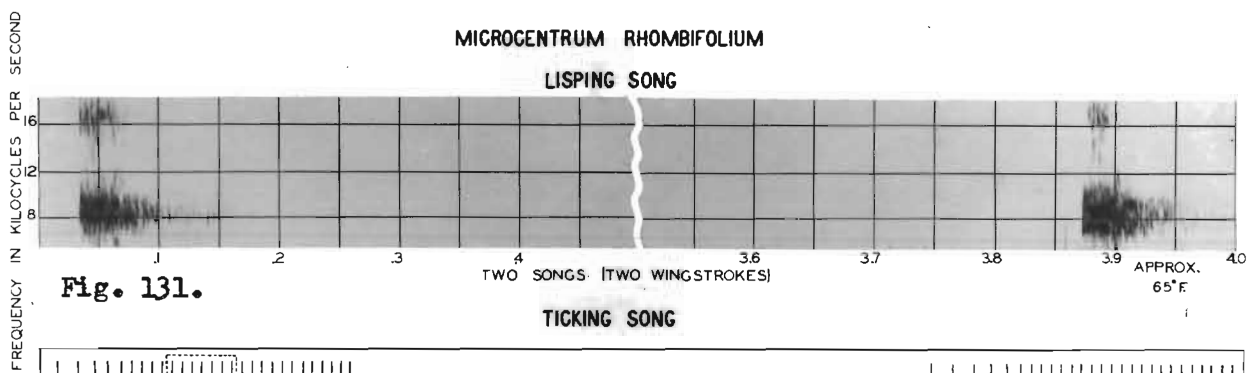


Fig. 131.

TICKING SONG

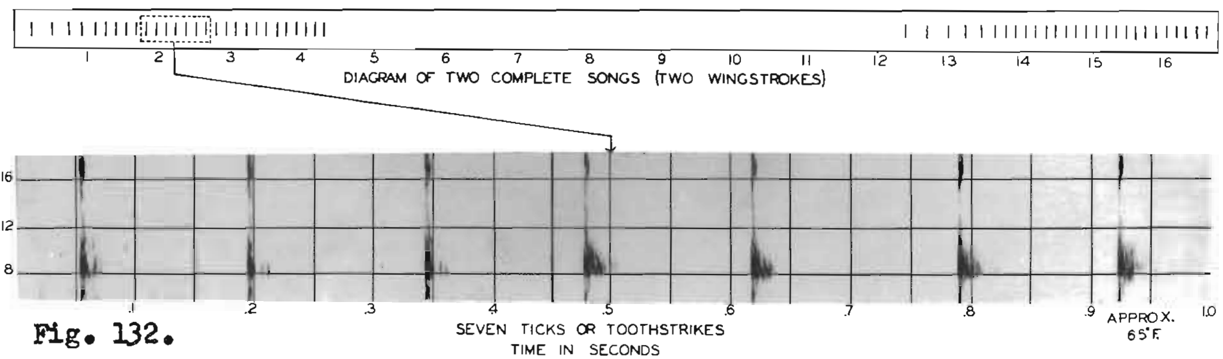


Fig. 132.

produced by single wingstrokes at regular intervals of about 3-5 seconds. However, the sweep of the file across the scraper, or the acoustically effective movement of the tegmina (apparently closing) is done so slowly that each toothstrike appears as a separate pulse. The result is a series of 15-30 toothstrikes requiring 4 or 5 seconds to be delivered. This appears to the ear as a series of loud, sharp ticks which are produced most rapidly near the center of the series. The last 2 or 3 ticks are often run together.

Fulton (1932, 6) describes the lisping song with intervals of 2-3 seconds, and the ticking song as lasting about 2½ to 3 seconds with the ticks delivered at about 7 or 8 per second.

<u>Microcentrum retinerve</u> (Burmeister)

The Angular-Winged Katydid

<u>Distribution</u>

This species is southern in distribution, Columbus, Ohio, being the most northern point at which it has been collected during the present study. Blatchley (1920, 6) records it from the southern third of Indiana, Plummer's Island, Maryland, Kentucky, Tennessee, Georgia, and Florida in eastern United States. Hebard (1934, 6) cites Jonesboro, in extreme southern Illinois, as a northwestern record and gives other western limits as Polk County, Arkansas, and Bowie County, Texas, stating that the Nebraska and Kansas records of Bruner, cited by Blatchley are incorrect.

In Ohio this species has been heard most often in trees along river banks and in swamp forest associations. It has also been heard in the oak forests along the ridgetops in Hocking County, Ohio. Friauf (1953, 26) lists this species from both mesic and xeric hammocks in the Welaka area in northern Florida. At Raleigh, North Carolina it was heard on August 9 in the trees around a farm pond.

At Columbus, Ohio, this species does not begin singing until early August, being one of the last of the Orthoptera to mature. Blatchley records adults between August 20 and September 26 in southern Indiana.

Singing Behavior

This is a night-singer which is generally found only in the tops of tall trees. It is very difficult to capture. On one occasion in August, 1955, two individuals appeared in the Ohio State University Veteran's Housing area, and were captured singing on the sides of buildings near lights, about ten feet from the ground.

The song is repeated at such wide intervals that it is difficult to assess its regularity, and to record it. The only clear recording obtained of this species was a result of simply aiming the parabolic reflector into a swamp forest where these insects were singing in abundance, and allowing the tape recorder to run. After about 5 minutes an individual by chance located several yards away in front of the parabola sang, and a clear recording resulted.

Song Records

*Pickaway Co., O. (Pickaway Twp.) 10 Sept 1954, 63° F., 1 min. 43 sec., 6 double-phrase songs of 3 individuals.

Song Description and Analysis

The song consists of 2 (rarely 3) loud phrases repeated about 2 or 3 seconds apart (at 65° F.) (Plate XLVI). Each phrase is composed of 2-7 pulses delivered at a rate of 6-7 per second at 65° F. The second phrase usually contains 1 or 2 fewer pulses than the first, and thus gives the impression of an echo. Common sequences are 7 - 5, 6 - 4, 5 - 3, and 4 - 3 pulses per phrase.

The song is loud, harsh, and lisping in quality, very reminiscent of *Scudderia* sounds.

This song has been well described by Allard (1910c, 6, and 1928a, 6), probably from around Washington, D. C. His description varies from the above only in that he says the usual number of phrases is 3, rather than 2 as heard by this writer in Ohio and at Raleigh, North Carolina. Allard says that less rarely, 4 may be given, and at low temperatures only 1 phrase may be delivered. He says further, "The song is given irregularly usually not oftener than 1-3 in a minute."

Pterophylla camellifolia camellifolia (Fabricius)

The Northern True Katydid

Distribution

This is the northern form of *Pterophylla* in eastern United States, extending to somewhere along the southern border of the Appalachians. According to Rehn and Hebard (1916, 6) it merges with *Pterophylla camellifolia intermedia* (Caudell) in the Georgia Piedmont and the Coastal Plain. In the present study, individuals recorded and heard from Lenoir to Raleigh, North Carolina, had a much faster and otherwise different song from individuals recorded and heard in the northern states south to Dickenson and Bath Counties, Virginia (Plate XLVII). Rehn and Hebard also state that the song they heard in southeastern United States was much quicker and sharper than that of the northern insect, and that the individuals involved probably belonged to *intermedia*. However, Hebard (1941, 6) says that *intermedia* does not extend east of Biloxi, Mississippi. The characters that Rehn and Hebard give to separate *intermedia* and *camellifolia* are those given by Caudell, involving the structure of the male cerci. These are difficult to compare without seeing the type specimens, since they are of a somewhat relative nature, but it appears that two males sent to me by Dr. B. B. Fulton from Raleigh, North Carolina, could be *intermedia*, while the northern specimens I have from Illinois and Ohio appear to correspond to Caudell's figures of *perspicillatus* (*camellifolia*). Another character noted in the few specimens

PLATE XLVII.

PTEROPHYLLA CAMELLIFOLIA

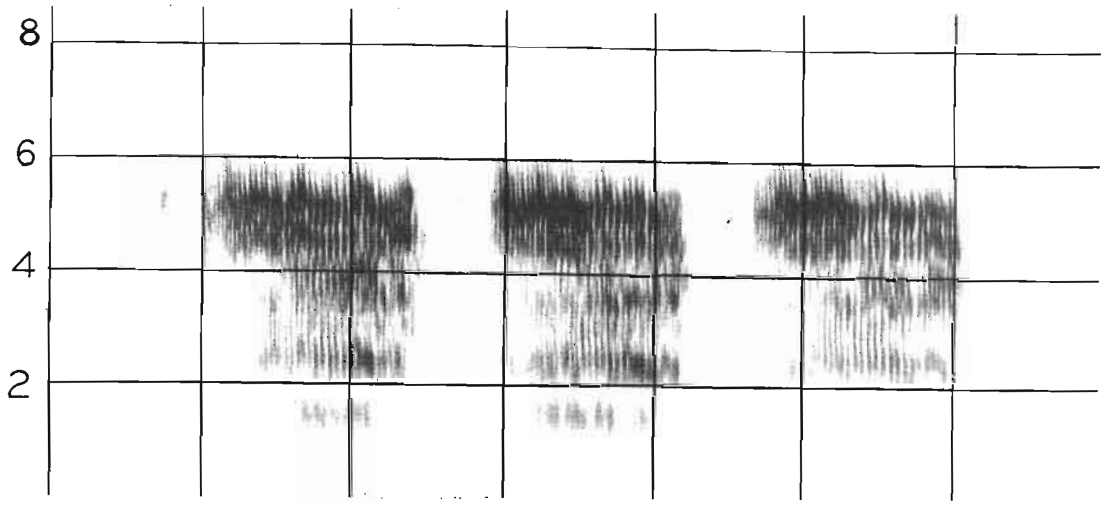


Fig. 133. NORTHERN

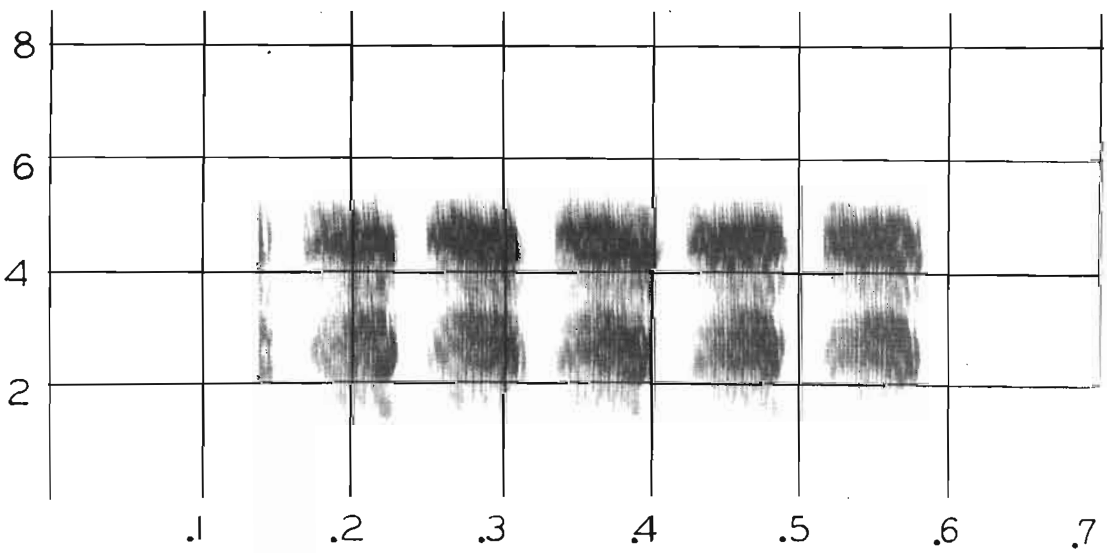


Fig. 134. SOUTHERN

examined which seemed of a more objective nature, was the structure of the subgenital plate. Rehn and Hebard mention that this plate is wider in _intermedia_ than in _camellifolia_, giving a figure of 2.6 mm. for _intermedia_. In my Raleigh specimens this plate is 2.3 mm. wide at its widest point, while in an Ohio specimen it was only 2.1 mm. wide. However, in the Ohio specimen the narrowest portion of this structure, basad to the distal enlargement, was 1.7 mm. wide, while in the North Carolina specimen it was only 1.3 mm. wide. The ratio of the width of the narrowest portion of the subgenital plate to the widest portion is .81 in the northern specimen, while in the southern specimen it is .57. Examination of more specimens is needed, and especially specimens from where these two song forms meet, to determine whether this is a clinal variation, or two distinct species are represented. In the present paper these forms will be treated as subspecies, and the name _intermedia_ used tentatively for the southern form.

At Columbus, Ohio, _camellifolia_ matures in late July and can be heard until frost in tall trees, both in lawns in the city, and in forests, wooded fencelines, and osage hedgerows outside the city. It seems to occur more abundantly in damp forests than in well-drained hillside or ridgetop woods.

Blatchley (1920, 6) reports hearing the song of this species as early as July 10 in Crawford County, Indiana, and as late as October 27. Hebard (1934, 6) cites records between July 23 and October 27 in Illinois. Rehn and Hebard (1916, 26) cite records between July 16 and October 1 for Plummer's Island, Maryland.

Caudell cites a song record for the first week of November for the same locality. Hebard (1938, 6) says adults appear late in July in Pennsylvania, in deciduous treetops and are never seen near the ground until after fall sotrms or when females are ovipositing in the bark of trees. Hubbell (1922, 6) heard this species during the late summer and fall high among the brances of large trees in Michigan.

Singing Behavior

This is a night-singing species, beginning in late dusk, and continuing until sometimes after midnight. In Dickenson County, Virginia, individuals were heard all night long until about 4 A. M., although most had stopped singing an hour or two before this. Singing males are usually very near the tops of the trees, and only rarely less than 20 feet from the ground. They perch either on top of a more or less horisontal branch or on a vertical trunk.

Singing males are generally not in the same tree, or at least in the same part of the same tree, and individuals remain in or near one tree, or even one part of a tree, for long periods of time, perhaps their entire adult life in some cases. The location of singing individuals in the trees in a lawn or patch of woods can be plotted and then predicted night after night with accuracy.

Starting or stopping of song by an individual seems to cause a similar reaction in its neighbors, and a sort of imperfect alternation sometimes results. Two individuals may alternate their songs for several repetitions, then suddenly sing together, or slight differences in their rates may cause them to alternate, sing together, alternate, etc. On one occasion in the mountains of Pocohontas County, West Virginia, tremendous numbers of katydids were singing and this singing at first appeared to be synchronous since there were definite pulsations in the intensity of the sound, which was so loud as to interfere with ordinary conversation. However, upon later checking a recording made by sweeping the parabola in a slow arc, it was discovered that these pulsations in the sound occurred at twice the rate of song of a single individual, indicating that actually a synchronized alternation was occurring. Individual A was alternating songs with individual B, individual C was alternating songs with A, thereby synchronizing with A, etc., or apparently so.

This katydid is possibly a unique orthopteran in North America since it produces a "protest" sound, that is, it stridulates when captured and held (if the tegmina are free), opening and closing its tegmina repeatedly. In many orders, such as Coleoptera, Hemiptera, Homoptera, Hymenoptera, and Lepidoptera, such "protesting" is well-known, and often the only sound response known, but it is rare in Orthoptera.

This continuous repeating of sound pulses in situations involving disturbance or capture has a relationship with what appears to be a "fight" or "challenge" sound. On Bald Mountain in Bath County, Virginia, the usual number of pulses per phrase in the song of <u>camellifolia</u> is 3-6 (observed in August, 1955). On August 19, 1955, however, two males were heard alternating phrases of unusual length.

Closer observation revealed that these two males were only a few feet apart in a rather small tree. Their songs were recorded and observed over a period of several minutes. One male would produce a phrase containing from 15-25 pulses, and the other would immediately follow suit, so that the impression was left that they were trying to "out-argue" each other. This may sound unduly anthropomorphic, but it is a point of interest that in a great many cases, the differences between the sound made by different species of insects, birds, and mammals (including humans) in the territorial, calling, solitary, or whatever-you-want-to-call-it situation (perhaps ordinary conversation in humans) and that made during a fight or during courtship are analogous in many respects. Faber (1953, 6) first noted this relationship between the sounds of birds and insects.

Caudell (1906, 6) was the first to note the protest sound in this species, obtaining it from the female, which he says stridulates in a manner similar to that of the males, producing a sharp, scraping note easily heard for several yards. He did not observe this sound except in females being handled, and apparently no one else has heard female katydids stridulate.

In Dickenson County, Virginia, on August 6, 1955, it was noted that when individuals started singing in the evening; they often delivered a phrase containing 25-30 or more pulses, then settled down to their rhythmical singing of 3-4 pulse phrases. In Ohio and Illinois the first few phrases of an individual beginning to sing often contain only one pulse.

Pierce (1948, 26) conditioned a male of this species to sing in the laboratory by first playing before this male a recording of his own song. After passing through more and more crude imitations, he eventually got this male to the place where he would give a "phono-response" to almost any "loud and raucous noise," and his answer would contain "more or less accurately" the same number of pulses as in the stimulating sound, up to 5, beyond which he seemed to "lose count."

More evidence concerning the effect of the song of an individual upon his neighbors was discovered upon playing back the recording made of the two males "arguing." Careful listening revealed a third individual in the vicinity that was singing a regular 3-4 pulse song; he was apparently stimulated by those two "arguing" individuals which were close by, and was delivering his phrases in synchrony with the first 3-4 pulses of each song of each of the "arguing" individuals. Thus he was "alternating" with both individuals, due to the unusual length of their individual phrases, alternately synchronizing with one individual and alternating with the other, then vice versa.

The northern true katydid is not capable of sustained flight, but captured individuals will spread their tegmina and glide if dropped or thrown into the air. Several times, while climbing a tree for a specimen, I have seen individuals glide from a high branch to a lower one, or to the ground, after their perch had been jarred.

Song Records

The calling song has been heard continuously from late July until frost at Columbus, Ohio, during the two seasons of this study, and at every other locality visited between these dates.

*Jefferson County, O. (Bergholz) 15 Aug 1954, 65° F., (1) 22, 2-pulse phrases in 40 sec. (2) 47, 1 and 2-pulse phrases in 90 sec. (3) 26, 2-, 3-, and 4-pulse phrases in 50 sec.

*Franklin Co., O. (Clinton Twp.) 6 Aug 1954, 63° F., 32, 2- and 3-pulse phrases in 53 sec. (2) 28 July 1954, 74° F., 2-, and 3-pulse phrases (2 individuals singing), and about 1 phrase per second for 65 sec. (3) 23 Sept 1954, 59° F., 53, 1- and 2-pulse phrases in 123 sec. (4) 25 Sept 1954, 75° F., 40, 2-pulse phrases in 50 sec.

*Hocking Co., O. (Ash Cave) 11 Sept 1954, 65° F. (approx), 29, 1-pulse phrases in 60 sec.

*Franklin Co., Ky. (Walker) 14 July 1955, 78° F., 26, 2-pulse phrases in 30 sec.

*Dickenson Co., Va., 6 Aug 1955, 34, 2-pulse phrases in 24 sec.

*Bath Co., Va., 11 Aug 1955, 65° F., 14, 4-, 5-, and 6-pulse phrases in 33 sec.

*Pocohontas Co., W. Va., 75° F., 13, 3-pulse phrases in 20 sec.

*Lyon Co., Ky. (Walker) 25 Sept. 1955, 23, 2-pulse phrases in 32 sec.

*Crenshaw Co., Ala (south of Brontley on U. S. 331(Walker)), 15 Sept 1955, 2-pulse phrases at a rate of 1 in 1-2 sec.

*Piatt Co., Ill., 5 Sept 1955 (temp. not recorded) (1-3) 3 specimens together, 55-65° F., 77 sec., 1- and 2-pulse phrases at rate of 1 every 2-3 seconds; (4) 58° F., 21, 1-pulse phrases in 21 sec.; (5) 65 F., 31, 1-pulse phrases in 30 sec. (6) 20, 2- and 3-pulse phrases in 27 sec. (7) 108, 1-pulse phrases in 57 sec.

*DuPage Co., Ill., 13 Sept 1955, 78 F., 8, 3-pulse phrases in 9 sec.

<u>Song Description and Analysis</u>

This song (Plate XLVII) is a regular repetition of loud, coarse, multi-pulse phrases at rates varying from 30 to 85 per minute, depending on the temperature, the number of pulses per phrase, and the kind of stimulation by neighboring individuals. The fewer pulses per phrase, the faster the pulse rate. An individual alternating with an erratic singer will often place his own phrases where those of the other individual would occur if he were singing regularly and the two were alternating perfectly. This causes the dominating individual to produce more phrases than if he were singing alone at a regular rate.

Around Columbus, Ohio the phrases usually contain 2 pulses, but individuals have been heard which consistently produced 1-, 2-, 3-, 4-, 5-, 6-, and rarely, 7-pulse phrases, as well. In Virginia and West Virginia the usual number of pulses was 3, 4, or 5; 2-pulse songs were rarely heard. In both Ohio and Illinois, however, colonies were heard in which most of the individuals were producing 4- and 5-pulse phrases. The pulse rate in the calling song is 4-5 per second at 75° F.

The song of this species has been described by a large number of authors, among them the following:

Snodgrass (1923, 6, Washington, D. C. and Wallingford, Conn.)
Fulton (1932, 6, 1934, 6, North Carolina)
Blatchley (1920, 6, Indiana)
Scudder (1874, 6, Springfield, Massachusetts)
Pierce (1948, 6, Franklin, New Hampshire)
Hayward (1901, 6)
Allard (1910d, 6, Towns County, Georgia)

The difference in the songs of northern and southern Pterophylla was noted by Snodgrass, and also by Dr. E. S. Thomas (personal communication), and it is mentioned by Cantrall (1943, 6).

Pierce got a pulse rate of about 5-6 per second and toothstrike rates of 278 and 254 per second, with no temperatures given. He says the usual number of pulses per phrase is 2. He obtained a practically continuous frequency spectrum from 18 kilocycles per second up to 63 kilocycles per second, and states that there are probably frequencies extending below 18 kps. all the way down to the tooth impact frequency. This is borne out by the Vibragrams in Plate XLVII. Pierce also states that the sound is made during the closing of the wings, which is rather easily observed by eye in the protest sound due to the fact that this species moves its wings so slowly. Hayward (1901, 6, Milton, Mass.) counted chirp rates varying from 18-to 19 per minute at 60° F. to 89 per minute at 82° F.

One specimen of this species was recorded with his tegmina intact, then successively as the tegmina were successively trimmed, piece by piece, until only the file and scraper remained. The chief difference in the sound, as revealed by listening and by examining Vibragrams, was in the intensity. It became successively softer as more of the tegmina was trimmed off, until in the last recording, when only the file and scraper remained, the sound was very faint, and the record gain had to be turned all the way up to register it well with the insect held only a couple of inches from the microphone.

Pterophylla camellifolia intermedia (Caudell)

The Southern True Katydid

As already mentioned, this katydid extends north to somewhere below the Appalachian Mountains, where its meeting or overlapping with *camellifolia* s. str. has not yet been studied. In the present study it was heard only during the August 1955 trip to North Carolina. Thomas Walker recorded its song in Holmes County, Florida, on September 15, 1955. Fulton (1951, 6) gives its song period at Raleigh as from early July to mid-September. No differences in its ecology or singing behavior were noted as compared with *camellifolia*.

Song Records

*Lenoir, N. C., 7 Aug 1954 (temperature not recorded) (1) 45, 4- and 5-pulse phrases in 48 sec. (2) 23, 4- and 5-pulse phrases in 31 sec., pulse rate 13 per second.

*Raleigh, N. C., 8 Aug 1955, 79° F., 23, 4- and 5-pulse phrases in 19 sec., 11.1 pulses per second within phrases.

*Holmes Co., Fla. (Walker) Sept 1955, 70° F., 33, 2-, and 3-, and 4-pulse phrases at a rate of 1 every 2-3 sec., pulse rate 10 per second.

Song Description and Analysis

The chief differences between this song and that of *camellifolia* are that the pulse rate (wingstroke rate) is faster, and the sound is less coarse or harsh-sounding, probably a little softer. As shown in Plate XLVII, the toothstrike rate within the pulses is about the same in the two forms. Most *intermedia* have more pulses per phrase than most <u>camellifolia</u>, but there is almost a complete overlap in this character. The phrase rate or chirp rate is about the same between the two forms. It remains to be seen whether extensive recording and collecting along the line where these two forms meet or overlap will reveal intermediates in song and in the morphological characters discussed above.

Tettigoniidae, Copiphorinae

The Coneheaded Grasshoppers

Only one northeastern species in this subfamily has not been recorded during this study, <u>Neoconocephalus</u> <u>triops</u>, the only singing Orthopteran in Ohio which overwinters in the adult stage. According to Dr. E. S. Thomas, this species has been collected in Adams County in southern Ohio. He describes the song as a continuous buzz, much like that of <u>N</u>. <u>retusus</u>, <u>palustris</u>, or <u>robustus</u> <u>crepitans</u>. It probably sings from early May until early July in southern Ohio.

The other eight species included here apparently all overwinter in the egg stage and produce but one generation per season. The earliest to mature at Columbus, Ohio, is <u>N</u>. <u>ensiger</u>, which begins to sing in early July.

All the northeastern species are night-singers, although <u>N</u>. <u>retusus</u> often begins singing before sundown, and <u>N</u>. <u>ensiger</u> colonies commonly start up for brief periods after rain showers, or on dark, cloudy days.

All of these species occur chiefly on herbaceous vegetation, and the singing males are generally found perched near the top of the vegetation, most often in a vertical position on a stem, either head up or head down. Both sexes apparently spend the day near the ground, and are usually found with the head buried in the ground cover. When the males begin singing in the evening they sing in short bursts, starting near the ground and gradually working upward until they reach somewhere near the top of the vegetation. When disturbed, singing males either fly, or more often, drop to the ground where they remain motionless with the head down, often buried in the ground cover. The males are sedentary, and are rarely found closer together than 3 or 4 feet when singing. Their songs are loud buzzes, continuous in 6 species, broken at regular intervals, or "intermittent," in two others, and _N. ensiger_ has a unique, continuous, lisping song.

No song other than the calling song has been observed in coneheads, except for a slight alteration of song by a male _N. nebrascensis_ upon agitation of his perch, and a peculiar crackling noise made by a caged male of _N. robustus crepitans_, while walking around the cage. Apparently, neither copulation nor courtship have ever been described for species of _Neoconocephalus_.

Those species that have regularly broken or "intermittent" songs synchronize.

Neoconocephalus ensiger (Harris)

The Sword-Bearing Conehead

Distribution

This is a northern species, extending southward to the southern border of the Appalachians. Rehn and Hebard (1914, 26) give its distribution as from Norway, Maine, across southern Ontario to Minnesota, Bismarck, North Dakota, then south to Colorado and the Rio Grande River in New Mexico. They state that little is known of the southern limits of the species' range. Fulton (1932, 6) says it occurs only in the mountains in North Carolina.

At Columbus, Ohio, this species matures in early July and sings until frost. It is found in grassy and weedy fields and roadsides, but is most common in marshy or poorly-drained areas. Around Columbus, Ohio, it is the most common species in the genus, and is heard practically continuously along the roadsides at night. In Piatt County, Illinois, however, it is difficult to find, being apparently limited to small colonies, spottily distributed. One such colony occurs in the swales along U. S. Route 10 near the Champaign-Piatt County line.

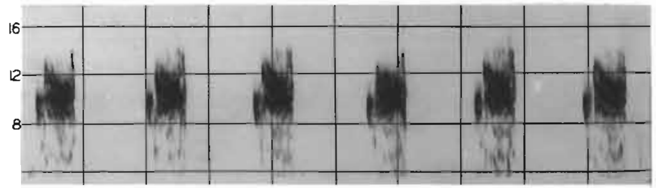
Blatchley (1920, 6) records adults "about July 10" in central Indiana, with an adult female taken in Vigo County on June 8. Hubbell (1922, 6) found adults between August 30 and September 8 in Michigan, in fields of second-growth scrub, shrubbery along roadsides and in margins of woods, thickets of tall weeds and bushes, tall grass in fields and pastures, corn and wheat fields, and lizard's tail and sedge marshes. Hebard (1938, 6) says adults appear in early July in Pennsylvania and prefer dry unland pastures and cultivated fields. Cantrall (1943, 6) found adults from July 11 to September 4 on the George Reserve, Michigan, in heavy growths of vegetation along the margins of marshes and swamps.

Singing Behavior

This night-singing species has been observed singing between 48° F. (in the field) and 85° F. (in the laboratory). A male was noted singing around midnight on a September night when the temperature was 50° F., and dropping rapidly. He sang continuously for the next 15 minutes, by which time the temperature had dropped to 48.5° F. (about 3 feet away on his level). At this point his song became irregular, and after about a minute of "stuttering," he stopped completely. No other singing insects could be heard in the area after he had stopped. A male Acheta (mountain) sang in a jar in the laboratory from 100° F. down to 48.5° F., when he stopped, and though the temperature was held within a degree of this temperature for about an hour, he did not sing further. When the temperature was allowed to rise several degrees, he began singing again.

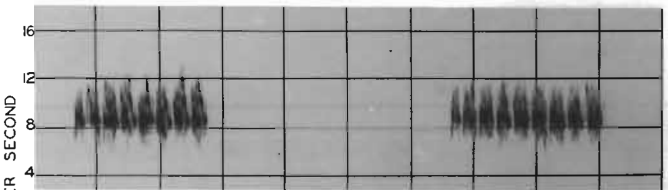
A rather dense and isolated colony of ensiger was observed for 8 nights between 26 July and 13 August 1954, and temperature, humidity, light intensity, and the time were recorded each evening when the colony began to sing. As shown in Plate XLIX, light intensity was the only one of these variables that remained somewhere near constant

PLATE XLVIII. SONGS OF NEOCONOCEPHALUS

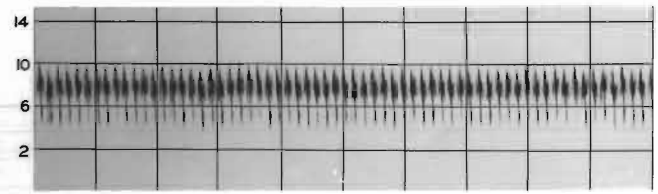


76° F.
Fig. 135. ENSIGER

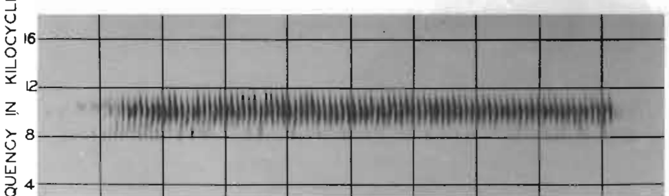
65 - 70° F.
Fig. 139. CREPITANS



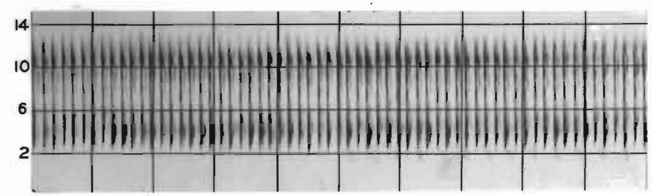
75° F.
Fig. 136. EXILISCANORUS



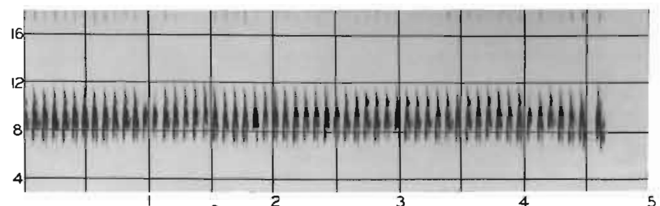
73° F.
Fig. 140. LYRISTES



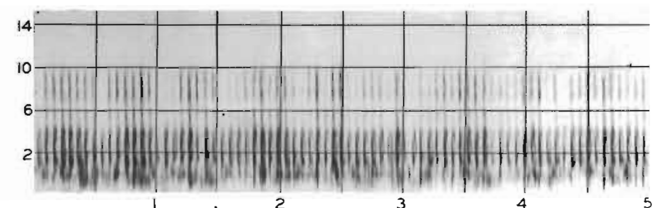
78° F.
Fig. 137. CAUDELLIANUS



73° F.
Fig. 141. RETUSUS



70 - 75° F.
Fig. 138. NEBRASCENSIS



70° F.
Fig. 142. PALUSTRIS

FREQUENCY IN KILOCYCLES PER SECOND

TIME IN SECONDS

PLATE XLIX. EFFECT OF ENVIRONMENTAL CONDITIONS ON BEGINNING OF SINGING BY AN ISOLATED, DENSE COLONY OF *NEOCONOCEPHALUS ENSIGER*

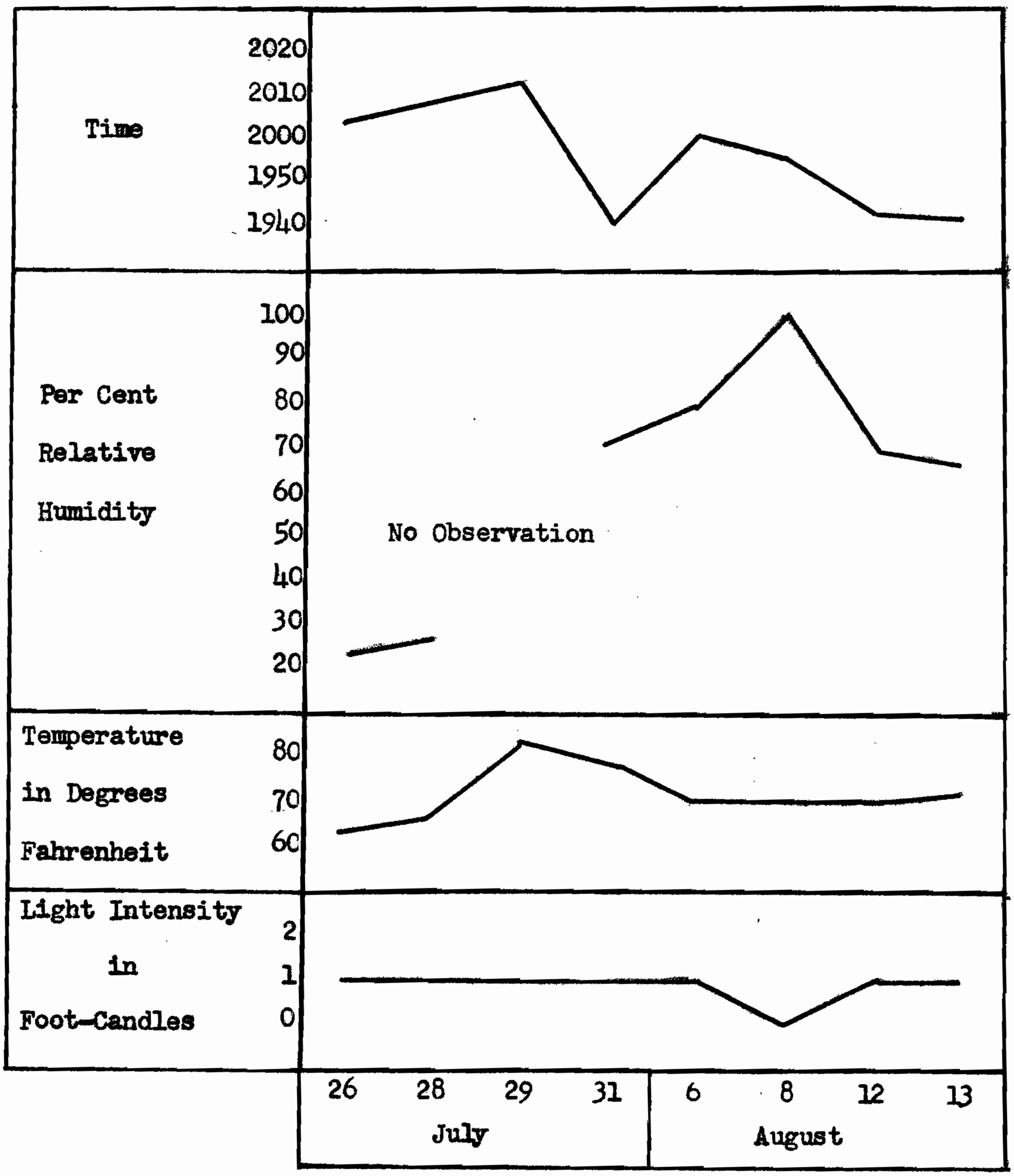


Fig. 143

Dates of Observations

from night to night at the time of starting of song by the colony. This was read at one foot candle for every evening but one when it was raining and the colony did not start until sometime after dark, perhaps after the rain had stopped. They were heard singing around midnight when it was not raining. This particular colony was well-suited for this study, since once any individual started singing in the evening, song was continuous all night, with other individuals joining the first within a few seconds after he began. This is not true in cases where the individuals of a colony are not close together, and apparently not when a colony is so situated that all the individuals are not under relatively uniform conditions, such as in a colony located along the border of the University Woods. In this case one individual often sang for several minutes before being joined, and sometimes, even after two or three individuals had started singing, the whole colony would stop singing for several minutes before starting up again. The same observations have been made on other species, though in some cases, such as *Oecanthus angustipennis* and *Neoxabea bipunctata*, there is a great deal of "faltering" or short bursts of singing in the evening by individuals before steady singing begins, even when the colonies are dense, isolated, and under fairly uniform conditions.

Apparently conditions other than light intensity are involved in the starting of song by *ensiger*. On three separate occasions colonies were heard apparently in full song in either bright sunlight, or on bright or dark, cloudy days. In Licking County, Ohio, at 11 A. M.

on August 13, 1954, a colony was heard singing after an all-morning drizzle of rain. In Williams County, Ohio, on August 19, 1954, a colony was heard at 5:30 P. M. on a sunny, clear afternoon. Near Medina, Ohio, on August 26, 1954, a colony of ensiger was heard singing at 7:05 P. M. with the sun still shining and the sky practically cloudless except for a slight haze around the sun. Two more colonies were heard along the road before 7:50 P. M., with the sun still up. In Wayne and Lancaster Counties, Ohio, on July 27, colonies were heard for 20-30 miles along the highway after a quick rain at about 3:30 P. M. The clouds moved on a d the sun shone brightly (about 5 P. M.), but ensiger continued to sing, perhaps as extensively as it usually does at night, all along the highway. A noticeable drop in temperature had occurred at the time of the storm. We continued to drive southward until well after dark, and apparently a complete stopping of song occurred between this unusual afternoon singing and the normal night-singing period. The fact that colonies once stimulated into song will continue singing even after conditions have returned to a situation which ordinarily would not stimulate beginning of song, gives an indication of the strong stimulatory effect the singing of one individual may have on others nearby.

Song Records

The song of this species has been heard continuously at Columbus, Ohio, from July until frost, during both seasons of the study.

*Franklin Co., O. (Clinton Twp.) (1) 24 July 1954, 60° F., 40 sec.

at 7.4 pulses per sec. (2) 9 July 1954, 60° F., 6.8 pulses per sec., 130 sec. (3) 25 Sept 1954, 70° F., 23 sec., at 11.6 pulses per sec. (4) Sept 1955, 88° F. (caged in lab.) 17.2 pulses per sec., 80 sec.

*Williams Co., O. (Northwest Twp.) 19 Aug 1954, 58° F., 23 sec. at 6.5 pulses per sec.

*Licking Co., O. (Buckeye Lake) 15 Sept 1954, 67° F., 62 sec. at 11 pulses per sec.

*Cuyahoga Co., O. (Berea) 26 July 1955, 76° F., (1) 20 sec. at 11.4 pulses per sec. (2) 32 sec. at 13 pulses per sec.

*DuPage Co., Ill. (Bemis Woods) 18 Aug 1954, about 70° F., (1) 17 sec. at 10.8 pulses per sec. (2) 70 sec. at 9.6 pulses per sec.

*Champaign Co., Ill., 5 Sept 1955, 57° F., 37 pulses per sec, 40 sec.

Song Description and Analysis

This song is a continuous repetition of rather loud, lispy pulses at rates, as shown above, between 5 and 15 per second, depending on the temperature (Plate XII). The dominant part of this sound is near the upper limit of the hearing range of many humans, and consequently to some people it appears as a rather soft sound. However, to a person with "normal" hearing, this sound can be heard 200-300 yards under favorable conditions.

This song has been described by a number of authors, including the following:

Davis (1887, 6, Staten Island, N. Y., 1891, 6, Moline, Ill.)
Beutenmuller (1894, 6, N. Y.)
Allard (1910b, 6, Oxford, Mass. (1928a, 6))
Rehn and Hebard (1914, 26) (quote Allard for Rhode Island)
Hubbell (1922, 6, Michigan)
Snodgrass (1923, 6, Washington, D. C.)

Fulton (1932, 6, North Carolina)
Cantrall (1943, 6, George Reserve, Michigan)
Pierce (1948, 26, Franklin, New Hampshire)
Borror (1954, 6, Maine)

There is not apparent disagreement between any of these descriptions and that given above, though Allard says the pulses are repeated 150-200 per minute, which would be slower than observed by this writer even at 48.5° F. (240 per minute). Hubbell suggests that singing individuals are more wary early in the evening than later in the night.

Neoconocephalus exiliscanorus (Davis)

The Slightly Musical Conehead

Distribution

This species has not been heard north of Franklin County, Ohio, in the present study and this is apparently a northern record. Rehn and Hebard (1914, 26) give its distribution as from New Haven, Conn. to Raleigh, N. C. on the east coast, and west to Thompson's Mills, Georgia, Dallas, Texas, and New Harmony, Indiana. Hebard (1934, 26) cites a Tower Hill, Illinois (south-central part of the state) as a northwestern record.

The first individuals to sing are heard in late July around Columbus, Ohio, and some individuals probably live until frost. It has been heard chiefly in marshy areas, but it is a strong flier, and scattered individuals are often heard along roadsides, in cornfields, bushes, and small trees.

Hebard (1938, 6) says adults appear in early July in Pennsylvania in high, weedy growth bordering marshes. Fox (1917, 6) found adults from August 9 to September 10 in tidal marshes (not salt) in Virginia, most commonly in tall reeds (Spartina cynosuroides) but "spreading in small numbers to the adjoining dry land (briery thickets, cornfields)." Davis (1887, 6) collected his type specimen among cattails on the salt marshes of Staten Island, N. Y.

Singing Behavior

This is a night-singer, like all the Neoconocephalus treated here, and is most often found perched 3-5 feet off the ground while singing. In dense colonies an "imperfect" synchronization occurs (notes actually broadly overlapping rather than perfectly synchronized), as with N. nebrascensis. These two species are the only species encountered in this study which sing from herbaceous vegetation and synchronize their songs. All the other "synchronizers" live and sing in trees.

Song Records

*Franklin Co., O. (Blendon Twp.) 16 Aug 1954 (cornfield) 144 buzzes (phrases) in 47 sec.

*Licking Co., O. (Buckeye Lake) 9 Sept 1954, 60° F., 54 buzzes 38 sec.

*Raleigh, N. C. (McCuller's Pond) 8 Aug 1955, 75-80° F., 47 buzzes in bursts at a rate of 1.8 per sec.

Champaign Co., O. (Cedar Swamp) 30 July 1955

Song Description and Analysis

The song is a steady and regular repeating of a loud, coarse phrase or buzz for indeterminite periods of time, and at rates of between 1 and 2 per second (Plate XLVIII). Each phrase contains 8-10 pulses, nearly indistinguishable to the ear and lasts only 0.1 or 0.2 second, being distinguishable from the buzzes of nebrascensis and caudellianus by this short length, and a coarse quality due to the slow pulse rate of about 70 per second at 75° F. This song is probably most closely related to that of ensiger.

The song of this species has been described by the following authors:

Allard (1910c, 6, Washington, D. C., 1928a, 6, 1918a, 6, Vinson Station, Va.)
Davis (1887, 6, New Jersey)
Rehn and Hebard (1914, 26, Atlantic Coast)
Beutenmuller (1894, 6, New York)

All of these descriptions agree essentially with that given above. Rehn and Hebard, however, say that the phrases are produced in series of 26 - 14 - 20 - 20 - 17. Allard (1918a, 6) also says that 15-30 consecutive notes are produced, followed by a brief pause. In the Ohio specimens recorded above, the singing was continuous and regular for the length of the recordings, 144 phrases in one case and 54 in the other. The North Carolina specimen was singing very erratically, producing from 1 to 6 phrases, then stopping for a few seconds. He may have been disturbed by our approach through tangled undergrowth and vines.

Neoconocephalus nebrascensis (Bruner)

The Nebraska Conehead

Distribution

This species is known from Ohio (Thomas, 1933, 6), Indiana (Blatchley, 1920, 6), Moline to Charleston, Illinois (Hebard, 1934, 26), eastern Nebraska, Illinois, Iowa (Bruner, 1891, 26), northeastern Kansas, St. Louis, Missouri (Rehn and Hebard, 1914, 26), Michigan (Hubbell, 1922, 6), and Bourbon County, Kentucky (Thomas Walker, personal communication). In Ohio, Thomas (1933, 6) says that it is abundant in the south and very rare in the northern portions, and the northernmost record he gives is in southwestern Huron County. In the present study it was heard and/or collected in Franklin, Hocking, Fairfield, Licking, Delaware, Champaign, and Pickaway Counties, Ohio, Dickenson County Virginia, and Piatt and Champaign Counties, Illinois. In central Illinois it is heard continuously along the highways at night, replacing *ensiger*, the most abundant species in Ohio, in these situations.

At Columbus, Ohio, this species begins singing in mid-July and can be heard until frost. At Buckeye Lake in Licking County, Ohio, and in Piatt County, Illinois, it was most abundant in marshy areas and along the border of swamp forest associations. In Hocking County, Ohio, a fairly dense colony was found in a bluegrass pasture on a well-drained slope. In Franklin County, Ohio, it is common in grassy and weedy fields.

Thomas (1933, 6) says this species "occurs normally in boggy spots in or near woodland, and in sloughs and river-bottom marshes bordered by willows and other trees. It seldom occurs far away from trees of some sort and in full fifty percent of the cases, we have found the singing males perched in woody vegetation." Hubbell (1922, 6) found adults of this species on August 3 in Michigan along the margin of a second growth scrub in the vicinity of bushes and shrubs, "rather close to the ground."

Singing Behavior

This species has never been heard singing before dusk. One colony, observed for several nights in the Ohio State University Woods in a small clearing, always began abruptly in the evening, without faltering. When the first individual started singing he was joined almost immediately by others and singing was then continuous into the night. Synchronization was effected from the start of song by the second individual. This is not perfect synchronization, but rather a slight delay is apparent after the beginning of a buzz by one individual before the buzz of another begins. This was also apparent in the synchronization effected by two caged males singing together.

Singing males are generally no less than 6 or 8 feet apart, though on 2 occasions, 2 males were noted singing about 2 feet apart. In these cases the 2 individuals were facing away from each other at about the same height on the vegetation and their songs were synchronized, except that one lagged slightly behind the other. When one individual was disturbed so as to cease singing, the other also stopped after producing two or three songs alone. If both were unmolested, when the first one began singing again the other joined in almost immediately. Two pairs of males caged together and observed intermittently over periods of several weeks, one pair in 1954 and one pair in 1955, exhibited all these behavioral characteristics many times. These males sang readily, although only six inches or a foot apart in the cages.

No actual "courtship song" has been observed in this species, but a caged individual changed his song (as described below) each time the screen upon which he was resting was agitated slightly, such as might be caused by the approach of a female on vegetation in the field.

Song Records

*Franklin Co., O. (Blendon Twp.) 31 July 1954, 85° F., 20 buzzes in 45 sec.

*Franklin Co., O. (Clinton Twp.) 25 Sept. 1954, 70° F. (1) 28 buzzes in 80 sec., (2) Sept. 1954, 20 buzzes in 45 sec.

*Champaign Co., O. (Cedar Swamp) 24 Aug. 1954, 73° F. (1) 44 buzzes in 95 sec., (2) 40 buzzes in 90 sec. (brown specimen), (3) 74° F., 26 buzzes in 63 sec. (brown specimen).

*Hocking Co., O. (Goodhope Twp.) 18 July 1954, 85° F., two specimens singing.

*Bourbon Co. Ky., 10 July 1955, 84° F., (1) 31 buzzes in 60 sec., (2) 6 buzzes in 14 sec. (brown specimen), and 5 buzzes in 19 sec.

Song Analysis

The song of the Nebraska conehead consists of a continuous repeating of loud, more or less uniform buzzes at a rate of about one in 2-3 seconds. The buzzes are a little longer than the intervals, and the song can be heard in the field at 200-300 yards under favorable conditions. Plate XLVIII shows the last part of one buzz of this song. The pulse rate is about 125 per second at 70-75° F.

This species has both brown and green color forms, and on three occasions it was noted in caged pairs that a green individual had a stronger buzz, of somewhat different quality, than that of the brown individual. On another occasion there seemed to be no difference in the songs of a green and a brown specimen heard together. The significance of these observations will depend on further investigation. Rehn and Hebard (1914, 6) mention a similar observation on Neoconocephalus triops at Thomasville, Georgia.

A caged male singing in the laboratory while perched on the screened sides of his cage, consistently split his buzz into two more or less equal parts each time the screen was jiggled slightly in an attempt to simulate the approach of a female. This kind of singing has never been heard in the field.

The song of this species has been described by the following authors:

Davis (1891, 6) Moline, Illinois
McNeill (1891, 6, Illinois)
Hubbell (1922, 6, Michigan)
Fulton (1928, 6, Iowa)
Thomas (1933, 6, Ohio)

All of these descriptions agree essentially with that given above.

Thomas (p. 306) gives an excellent verbal description, saying the song "consists of a series of buzzing notes of a lower pitch than that of lyristes. Each note lasts for a trifle more than one second and is followed by a pause of a half-second or less, the series of notes thus forming a rhythmical song which is continued for an indefinite period, thus: 'Bz-z-z-z-z-t, bz-z-z-z-z-t, bz-z-z-z-z-t, ...'"

Neoconocephalus caudellianus (Davis)

Caudell's Conehead

On August 10, 1955, a song was recorded near Raleigh, North Carolina, at a distance of perhaps 40 yards from the singer, using a parabolic reflector. The song was seemingly exactly like that of N. nebrascensis, with the exception that the buzzes were a little shorter, and produced at an obviously faster rate (1 plus per second at 78° F., Plate XLVIII). The pulse rate was 220 per second. The specimen was not captured, but the song was described in a letter to Dr. B. B. Fulton, and he expressed the opinion that it was almost surely N. caudellianus. Rehn and Hebard (1914, 6) describe the song of caudellianus as a "loud, resonant and constant dzeeeet-dzeeeet-dzeeeet, always the same, not rising and falling, the notes given deliberately, counted as averaging 12 in 10 seconds." This also fits the song recorded, and on this basis this recording has been tentatively identified as N. caudellianus.

Rehn and Hebard (1914, 6) record this species from New Jersey, South Carolina, Georgia, and Alabama. They say it is very widely distributed not only along the coastal strip in truck gardens, waste fields, and marshy fresh water areas, but also in boggy portions of the adjacent pine barrens and in fields there located. Rehn and Hebard, and Davis (1903, 26) mention the excellent flight ability of this species and its tendency to fly when disturbed.

<u>Neoconocephalus</u> <u>lyristes</u> (Rehn and Hebard)

The Lyrical Conehead

<u>Distribution</u>

Rehn and Hebard (1914, 6) say this species occurs in New Jersey and New York; their type was labelled "Chokoloskee, Florida" but they seriously question this label, stating, "... the dealer from whom the specimen was purchased is now known by us to be unreliable." Blatchley (1920, 6) claims to have a female from Palm Beach, Florida, which "agrees in all particulars with the type and New Jersey specimens except the color, it being a nearly uniform purplish-brown instead of green and in its having a slightly longer and more slender fastigium." Thomas (1933, 6) records lyristes from Ohio and quotes a letter from E. M. Walker (who compared Thomas' specimens with those he previously recorded as <u>nebrascensis</u> from Sarnia, Ontario (1904, 6), to the effect that his Sarnia specimens are undoubtedly <u>lyristes</u>. Thomas believes that some of Blatchley's (1920, 6) northern records of <u>nebrascensis</u> in Indiana are probably lyristes.

Rehn and Hebard state that <u>lyristes</u> "is locally common in New Jersey in bogs, fresh water marshes and in the coastal marshes in areas of Scirpus and high marsh plants near the mainland...." Thomas records adults between August 7 and October 6 in Champaign, Clark, and Miami Counties, Ohio, in "glacial relict bogs, showing a decided prairie influence in their vegetation. The species has invariably been associated with (although not always in) Shrubby Cinquefoil (Dasyphora fruticosa) and it has also been taken frequently on Big Bluestem grass (Andropogon furcatus)." He believes that lyristes "may have invaded the Great Lakes region from the Atlantic seaboard in early postglacial times by way of the Mohawk-Hudson outlet, over the same route believed to have been followed by a number of Atlantic coast plants."

In the present study, lyristes has been encountered only once, on August 24, 1954, at Cedar Swamp in Champaign Co., O., one of the localities given above.

Singing Behavior

This species began singing after the nebrascensis on the border of the swamp had already started on the one occasion that I observed it. The singing males were perched about three feet above the ground in shrubby cinquefoil. Thomas states that, "In our experience, the insect begins to sing in full sunlight late in the afternoon." Walker (1904, 6) reported the specimens recorded as nebrascensis singing in the morning hours.

Song Records

*Champaign Co., O. (Cedar Swamp) 24 Aug. 1954, 73° F., 60 sec.

Song Description and Analysis

The song of this species, like those of the following three species of *Neoconocephalus*, is a continuous buzz, kept up for an indeterminate length of time. It was so described by Rehn and Hebard (1914, 6), Walker (1904, 6), and Thomas (1933, 6). It is rather high and thin, easily recognizable from the buzzes of *robustus crepitans*, *palustris*, and *retusus*, by one who has heard all of them before. It has a relatively intense, narrow band of frequencies at about 7.5 kps., which gives it an almost musical sound, and accounts for its thinness. This sound can be heard 50-100 yards away under favorable conditions. The pulse rate is about 130 per second at 73° F. (Plate XLVIII).

Neoconocephalus robustus crepitans (Scudder)

The Crepitating Conehead

Distribution

Rehn and Hebard (1914, 6) state that typical *robustus* is found from Cape Cod, Massachusetts, to Philadelphia, Pennsylvania, and Ocean View, New Jersey. The line of intergradation of this form with *crepitans*, according to these authors, is "very unusually narrow," taking place in the vicinity of Ocean View, New Jersey, and on the Delaware River in the vicinity of Philadelphia, Pennsylvania, and on the fall line as far south as Washington, D. C. *Crepitans* extends from extreme southern New Jersey to Hastings, Florida, over the entire Mississippi valley region, with limits at La Porte County, Indiana, White Bear Lake, Minnesota, Garden City, Kansas, and Clarendon and Cisco, Texas, according to Rehn and Hebard (1914, 6). However, Hebard (1934, 26) assigned all the material from Illinois to typical _robustus_, and says, "It is becoming increasingly evident that this insect may be the response to a sand environment in this species and not the typical race elsewhere represented by a separable geographic race (_robustus crepitans_). We do not yet feel justified, however, in indicating synonymy." Later, in 1938, 6 (Pennsylvania), Hebard says of _crepitans_, "intergrading with _robustus robustus_."

In the present study this species has been encountered in Carroll, Williams, Champaign, Franklin, and Licking Counties, Ohio, DuPage and Piatt Counties, Illinois, Bourbon County, Kentucky (Thomas Walker), and Wake County, North Carolina. It was not collected in any sandy areas, and Dr. E. S. Thomas has referred all his Ohio specimens to _crepitans_ (personal communication). Therefore, since no variation has been noted in specimens collected in different areas, all the material treated here will be considered as _crepitans_.

At Columbus, Ohio, the crepitating conehead sings from mid-July until frost. Only one dense colony has been located during this study, and this was around Mud Lake in Northwest Township, Williams County, Ohio, in a rather poorly-drained, weedy pasture. In Franklin and Champaign Counties, Ohio, and Piatt and DuPage Counties, Illinois, records were limited to individuals heard and collected in both damp and well-drained grassy and weedy areas, or occasionally in stubble fields or cornfields. The individuals of this species are strong fliers.

Hubbell (1922, 6) found adults in Michigan on September 2 and 9 in tall grass and dewberry vines along a railroad embankment and in a low undergrowth of grass and small herbaceous plants in an open oak forest on a sandy ridge. Hebard (1938, 6) says adults appear in mid-July in high marsh vegetation and also in nearby upland grasses.

Singing Behavior

This is a night-singer, and singing males have been found all the way from only a few inches above the ground in low stubble, up to ten feet above the ground in an oak tree (DuPage Co., Ill.). Usually they are perched from 4 to 6 feet above the ground in tall herbaceous vegetation. I have never heard this species sing in the daytime, although Rehn and Hebard (1914, 6) say that typical *robustus* is "rarely heard singing lustily even on clear days as early as four o'clock. During the day males sometimes at long intervals give a short hesitating and irregularly harsh note which would not be readily associated with their song." They report a similar response in a Jamaican species of *Neoconocephalus*.

A caged male from Bourbon County, Kentucky, behaved in a rather peculiar manner. For long periods of time, sometimes in the day and sometimes at night, he walked "nervously" around the cage, back and forth and up and down, producing continuously a slight but definitely audible creaking noise. His tegmina were not in motion, and no other part of his body could be observed to move in such a manner as to indicate that it was responsible for the sound. This sound was recorded, and appeared on a Vibragram as an irregular succession of faint, sharp pulses.

Song Records

*Carroll Co., O. (Amsterdam) 14 Aug. 1954, temperature not recorded, 42 sec.

*Williams Co., O. (Mud Lake) 19 Aug. 1954, 30 sec., 65-70° F.

*Bourbon Co., Ky. (Thomas Walker, coll.) 14 July 1955, 75° F., 19 sec. (84 sec. of "creaking" recorded in lab. at 84° F.).

*Franklin Co. O. (Clinton Twp.) 19 July 1955, 79° F., 77 sec.

*Wake Co., N. C. (McCuller's Pond) 8 Aug. 1955, 76° F., 46 sec.

*Piatt Co., Ill. (Sangamon Twp.) 13 Sept. 1955, 65° F. (1) 35 sec. (2) 30 sec.

*DuPage Co. Ill. 13 Sept. 1955, 78° F., 55 sec.

Song Description and Analysis

This song is a very loud continuous buzz, lasting for indeterminate lengths of time. It is one of the loudest of North American insect sounds, and can probably be heard at least a quarter of a mile under favorable conditions. At a distance this sound has a high, whining quality, while up close it is dominated by a piercingly intense, smooth, low-pitched hum, possibly corresponding to the number of wingstrokes or sound pulses per second. As shown in Plate XLVIII, the pulse rate at 65-70° F. is about 190 per second. The pulses are apparently paired, and the wingstroke rate is probably 95 per second. Pierce (1948, 26) gives a pulse rate of 158 per second and a frequency of 7.16 kps. for a Massachusetts specimen which he identified as robustus robustus.

Many authors have described the song of "N. robustus" and "N. r. crepitans" and there is probably no way of knowing which insect was involved, since the song descriptions are essentially alike. The descriptions given by the following authors agree essentially with that given here:

Scudder (1893, 6)
Beutenmuller (1894, 6, New York)
Rehn and Hebard (1914, 6, New Jersey)
Allard (1916, 6, Clarendon, Virginia)
Fulton (1932, 6, North Carolina)
Pierce (1948, 26, Franklin, New Hampshire)

Allard describes two songs, and says, "the stridulations of this insect are somewhat puzzling." The second song he describes, "... a rather weak, continuous, snappy z-z-z-z-z-z-..." sounds much like the song of N. retusus. Scudder says this species sings "similarly by day and by night" and "... seems at a distance to be quite uniform; on a nearer approach one can hear it swelling and decreasing in volume, while there is a corresponding muscular movement of the abdomen backward, 2½ times a second." I have never observed this behavior in singing specimens.

Neoconocephalus palustris (Blatchley)

The Marsh Conehead

Distribution

This species, according to Rehn and Hebard (1914, 6), has been taken at New Brunswick, New Jersey, south to Raleigh, North Carolina, and westward from Vigo County, Indiana, south to New Orleans, Louisiana. Hebard (1934, 26) lists it from Lawrenceville and Carbondale, Illinois, giving these as northern and western limits.

In the present study this species has been encountered only twice, both times along a marshy stream running into Buckeye Lake in Licking County, Ohio. Hebard (1938, 6) says adults appear in Pennsylvania in early August, prefer grasses growing in swamps, and are "much less often found in marshes." He says it is known in Pennsylvania only from the swamps along the Delaware River in the southeastern part of the state. Fox (1917, 6) found adults from August 12 to October 2 in tidal marshes, on cattails, and in moist, grass-filled depressions at the head of gulleys. Blatchley (1920, 6) took adults between October 2 and 24 in Vigo County, Indiana, "... from the fallen grasses on the margins of a large lowland pond..."

Singing Behavior

The area where these males were heard during the night of September 9, 1954, was visited in late afternoon on September 15, 1954, to see if this species sang in the daytime. It was not singing, and did not begin until dusk. The singing males were perched 3-4 feet above the ground in cattails and smartweed.

Song Records

*Licking Co., O. (Buckeye Lake) 15 Sept. 1954, 70° F., 3 individuals, 1 min. 42 sec.

Song Description and Analysis

This song has little to distinguish it from that of the next species, N. retusus. It is a relatively soft, continuous buzz, often containing numerous "catches" or imperfections. Although softer than the songs of either of the two preceding species, it is audible at perhaps 50-100 yards, and is quite evident when heard along the highway at night. As shown in Plate XLVIII, the pulse rate is about 150 per second at 70° F.

Rehn and Hebard (1914, 6) give a song description similar to the above.

Neoconocephalus retusus (Scudder)

The Round-Tipped Conehead

Distribution

Rehn and Hebard (1914, 6) give the distribution of this species as from Connecticut south to Florida, west to Mississippi, Missouri, and Tennessee. Hebard (1934, 26) records it from central and southern Illinois, citing Urbana as a northern limit.

In the present study this species has been encountered in Franklin, Licking, Hocking, Fairfield, Pickaway, and Ross Counties, Ohio, Piatt and Champaign Counties, Illinois, and Wake County, North Carolina. Columbus is apparently the northern record in central Ohio.

At Columbus it sings from mid-August (or perhaps earlier) until frost. It is apparently the last of the coneheads to mature in this area. It is commonly heard in stubble and legume fields, pastures, and in marshes and other poorly-drained areas.

Rehn and Hebard state that this insect is an inhabitant of the grasses in waste fields, along the borders of marshes and in the drier portions of the marshes proper, and is usually to be found in large numbers. They cite records of adults between August 21 and October 23 for Pennsylvania and New Jersey. Blatchley (1920, 6) gives the dates August 27 to September 18 for Putnam County, Indiana, and Fox (1917, 6) found adults between August 23 and November 4 in Virginia, in the thick grasses of fields, pastures, meadows, and roadsides, and occasionally in or along the borders of tidal and other marshes. Hebard (1928, 6) says adults appear in mid-August in Pennsylvania in open lowland grassland.

Singing Behavior

This species is somewhat unique among Ohio Orthoptera in that although it seems a characteristic night-singer, it almost always begins singing earlier than any of the other species which do not sing by day. At 4 or 5 P. M., often when the sun is still shining, its "seedy" buzz will begin and continue into the night. This seems to be the rule in the species; one specimen, heard every evening for two or three weeks near my home in Columbus, invariably started 2 or 3 hours before the other night-singing species, although I never heard him sing earlier in the day.

Song Records

*Pickaway Co., O. (Pickaway Twp.) 10 Sept. 1954, 65° F., 3 min. 5 sec.

*Franklin Co., O. (Clinton Twp.) 24 Sept. 1954, 65° F., 98 sec.

*Piatt Co., Ill. (Sangamon Twp.) 5 Sept. 1955, 73° F., 32 sec.

Song Description and Analysis

This song is a thin, "seedy" buzz, audible from 50-100 yards under favorable conditions. It is probably the softest of the continuously buzzing songs produced by the Neoconocephalus treated here. The pulse rate, as shown in Plate XLVIII, is about 120 per second at 73° F.

This song has been described by Rehn and Hebard (1914, 6, New Jersey), Snodgrass (1923, 6, Washington, D. C.), and Fulton (1932, 6, North Carolina). None of these descriptions seems to differ significantly from that given above.

Tettigoniidae, Conocephalinae

The Meadow Grasshoppers

Introduction

Eighteen of the 35 species in this subfamily occurring in the United States and Canada have been recorded during the present study. Of the five species of Orchelimum not encountered, O. bullatum Rehn and Hebard has been taken in Lafayette, Indiana, by Fox (1915, 6, referred to O. nigripes erroneously, see Blatchley, 1920, 6, and Hebard, 1934, 26). The other four species, fidicinium Rehn and Hebard, militare R. & H., bradleyi R. & H., and superbum R. & H., are all limited to southeastern United States or to the Atlantic seaboard from New Jersey southward. Of the 12 species of Conocephalus not encountered, only one, saltans (Scudder), occurs within the area studied; all the rest are limited either to the Atlantic seaboard, or to the southern or western states.

Fulton (1932, 6) has described the songs of the 4 southeastern species of Orchelimum not encountered; Rehn and Hebard (1915, 6) give descriptions of the songs of O. bullatum and Odontoxiphidium apterum Morse; Pierce (1948, 26) analysed the song of C. spartinae (Fox); Caudell (1910, 6) describes the song of C. allardi (Caudell). Song descriptions for the remaining Conocephalus species are apparently absent from the literature.

Apparently all the northern species in this subfamily overwinter as eggs and produce one, or rarely two, generations per season. Fulton (1951, 6) believes that Conocephalus fasciatus fasciatus (DeGeer) has two generations at Raleigh, North Carolina. The earliest species to mature at Columbus, Ohio, are probably O. gladiator and C. fasciatus fasciatus, both of which have been heard in early July. The latter species was singing on June 15, 1955, at Carbondale and Cairo, Illinois.

All the species encountered in this study sing both day and night. Many seem to sing more at night than by day, and a few species of Orchelimum appear to sing a little differently at night than by day.

With the exception of _O. minor_ and _O. silvaticum_, all of these species are found on herbaceous vegetation. The _Orchelimum_ are generally perched from 3 to 5 feet above the ground, while the _Conocephalus_ species, ingeneral smaller insects, are usually found within 2 feet of the ground, often on plants only a few inches high. The singing males are usually perched vertically, and like the Copiphorinae, either head-up or head-down.

The songs of Conocephalinae are generally a combination of individual pulses and buzzes of various length, or involve two different speeds of wing motion. The song rhythms of 12 species are compared in Plate LI. Here the buzzes are shown as solid lines, and the ticks as vertical marks. The relationship of these diagrams to the actual songs can be compared by studying Plate L on which both diagrams and Vibragrams of the songs of the _Orchelimum concinnum_ complex are shown.

No song other than the calling song has been observed in Conocephalinae although males in close proximity often leave out all but the "ticks" or individual pulses of their song, or at least include more of these than usual. Apparently copulation has not been described for any North American species. None of the species treated here synchronize their songs, although in _O. nigripes_ two caged males alternated songs perfectly for long periods of time in the laboratory.

Orchelimum agile (DeGeer)

The Agile Meadow Grasshopper

Distribution

PLATE L. ORCHELIMUM CONCINNUM GROUP

Fig. 144. TYPICAL SINGING OF CONCINNUM AND DELICATUM

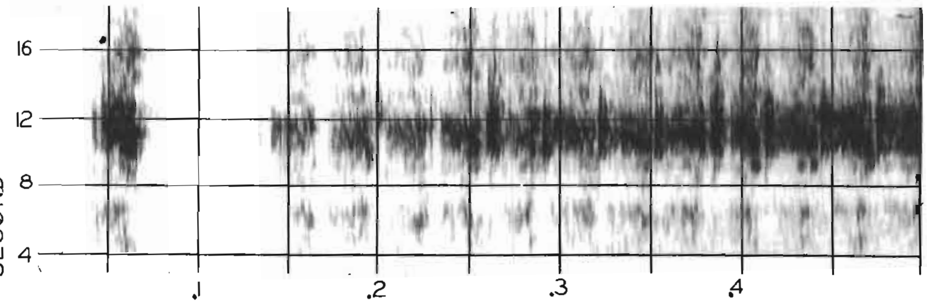


Fig. 145. CONCINNUM

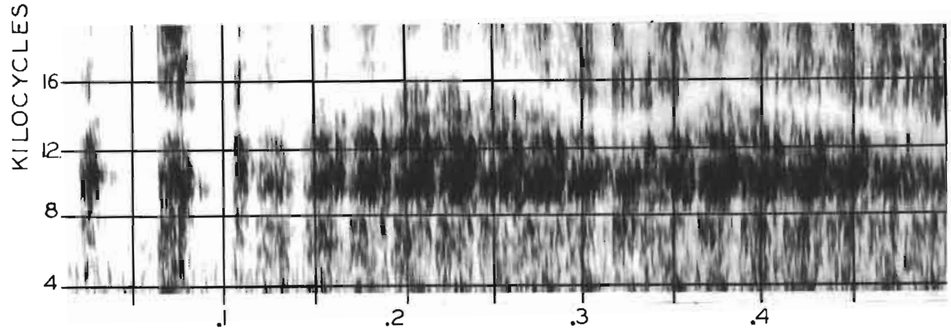


Fig. 146. DELICATUM
TIME IN SECONDS

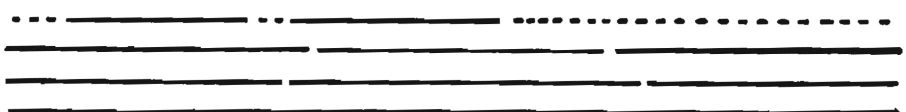


Fig. 147. TYPICAL SINGING OF CAMPESTRE

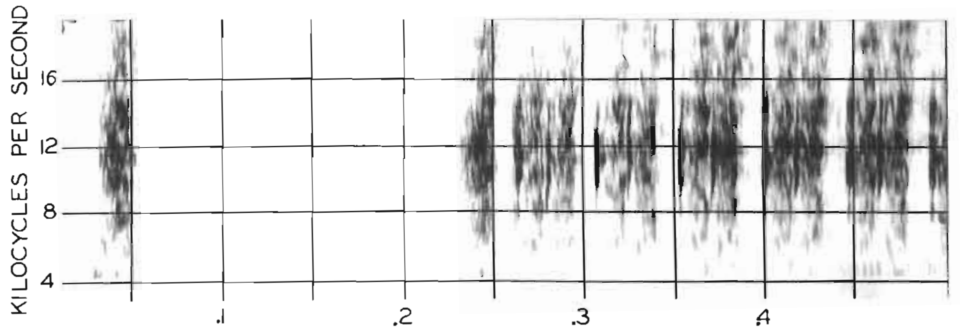
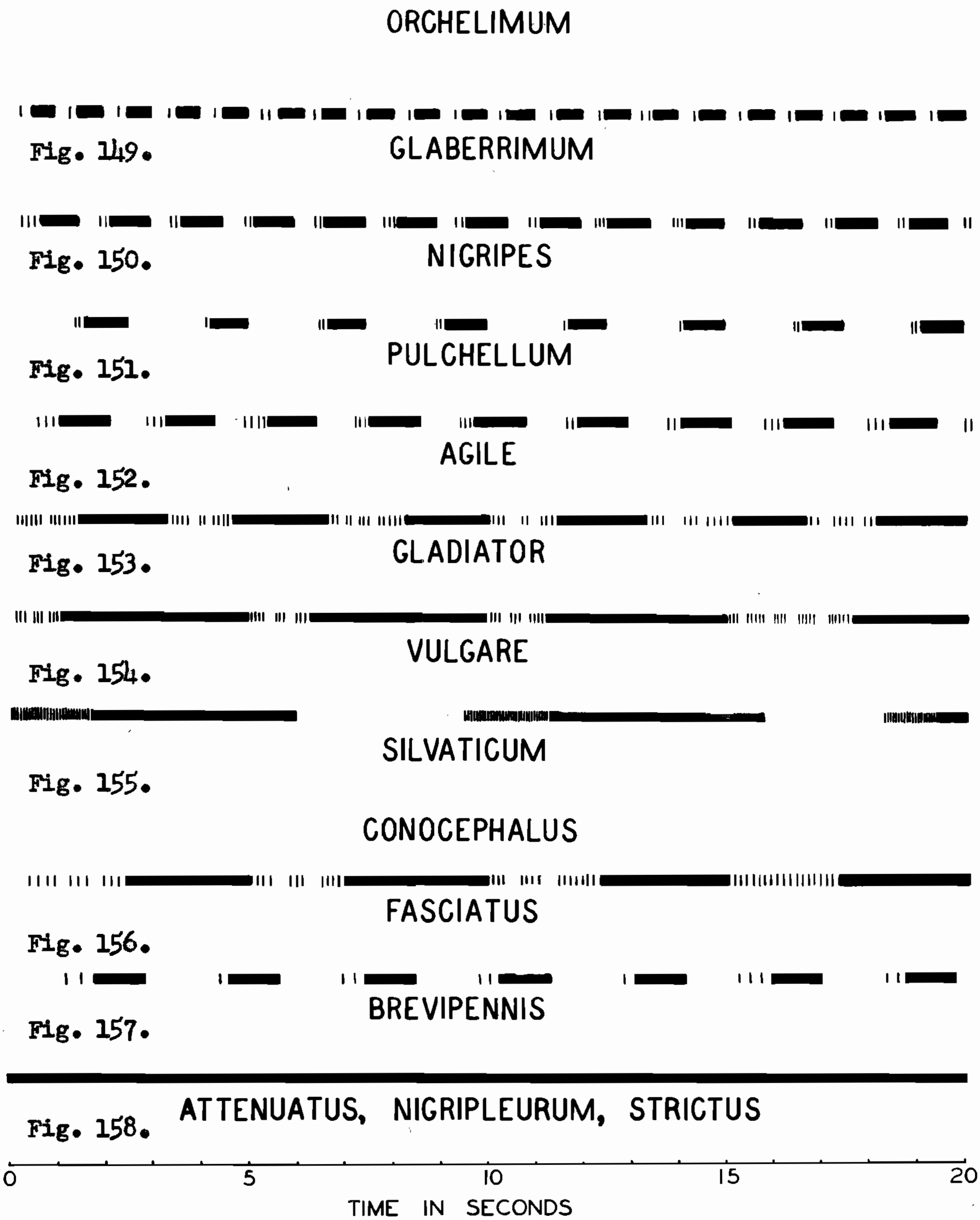


Fig. 148. CAMPESTRE
TIME IN SECONDS

PLATE LI. SONG RHYTHMS IN CONOCEPHALINAE



Rehn and Hebard (1915, 6) say this species occurs from southern Florida to southeastern Pennsylvania, west through southern Indiana (Blatchley (1903, 1920, 6), south-central Kansas, Arkansas, and Louisiana. They cite a record by McNeill for Rock Island, Illinois, but Hebard (1934, 26) does not list this species from Illinois. McNeill's (1891, 6) description of the song would indicate that he may have been referring to silvaticum or nigripes.

The only contact with this species in the present study was with a specimen captured by Thomas Walker in Jackson County, Florida, on September 15, 1955, and brought back and recorded in the laboratory. This specimen sang readily in the laboratory both day and night.

Song Record

*Jackson Co., Fla. 20 Sept. 1955, 80-85° F., 7 songs in 13 sec.

Song Description and Analysis

This is a fairly soft song, similar to those of O. pulchellum and O. gladiator. Three to four double-pulse ticks occur between buzzes at 3-5 per second. The buzzes last about one second and have a pulse rate of 204 per second.

Fulton (1932, 6) describes the song as similar to that of vulgare, but without the increase in intensity in the buzz, and also not so loud, and having perceptible pauses between the ticks and the buzzes.

Orchelimum glaberrimum (Burmeister)

The Red-Headed Meadow Grasshopper

Distribution

This is a southeastern species, extending from north-central New Jersey to southern Florida and inland as far as the Pine Barren region in New Jersey, Raleigh, North Carolina, and Macòn, Georgia (Rehn and Hebard, 1915, 6). In the present study it was recorded and collected August 8-11 from 12 miles south of Raleigh to 10 miles north of Durham, N. C.

Fulton (1951, 6) gives the seasonal song period of this species as from just past mid-July to November 1 for Raleigh, North Carolina. In 1932, he says of its habitat, "low places, on tall grass, weeds, bushes ..." Hebard (1938, 6) says adults appear in mid-July, presumably in New Jersey and Delaware, and are "... sure to be found in the bogs and wet meadows along the southeastern margin of Pennsylvania." Fox (1917, 6) found adults from September 5 to November 5, in the pine barrens of New Jersey, apparently restricted to inland bogs (cedar swamps), but in Virginia at Cape Henry he found it common in the rank vegetation of dune hollows and ditches and not infrequent in tall bunch grasses (Andropogon, Paniccim amarum, etc.) on surrounding dry dunes. He says it "evidently has a strong predilection for sylvan surroundings and further inland occurs in rank growth along ditches, woodland borders and scrub." In the present study this species was heard in several marshy areas, along roadsides in grassy and weedy areas, and in a stubble field.

Singing Behavior

This species sings both day and night. The singing males are usually perched from 3 to 5 feet above the ground, and neighboring individuals probably alternate their songs. This is a very wary species. The males stop singing, apparently upon seeing a moving object several yards away, and will not start up again for some time, often several minutes. Even males singing on vegetation which is waving violently in the wind stop singing when approached.

Song Records

*Raleigh, N. C., 15 Aug. 1955, 80-85° F., 3 min.

Song Description and Analysis

The song of this species is a characteristic 2-part meadow grasshopper song, containing both ticks and buzzes (Plate LI). One to three single-pulse ticks (usually one) are produced per buzz, at a rate of 3-4 per second. These are attached to the front of the buzzes which last about $\frac{1}{2}$ second and have a pulse rate of 64 per second. The whole phrase or song is repeated at a rate of about one per second in steady singing.

This is a fairly loud *Orchelimum* song, and is noticeable because of the sharp, short buzzes which can be heard several yards away. The song is probably most similar in structure to that of *O. nigripes*.

Fulton (1932, 6) describes this song similarly, giving the song rate as 16 in 10 seconds.

Orchelimum vulgare Harris

The Common Meadow Grasshopper

Distribution

This species is northern, apparently extending southward to somewhere just below the Appalachians, reaching to Thompson's Mills, Georgia, Raleigh, North Carolina, and north of the Carolinas extending to the coast, meeting or overlapping slightly with *glaberrimum* in New Jersey and North Carolina. Westward it extends to northeast Texas, Colorado, and Wyoming, and northward from Minnesota across Ontario, southern Quebec, and southern Maine (Rehn and Hebard, 1915, 6). In the present study it has been encountered at almost every locality visited between mid-July and frost, in Illinois, Indiana, Ohio, Kentucky, Tennessee, Virginia, West Virginia, and North Carolina. It is one of the most commonly encountered singing insects in Indiana, Illinois, and Ohio, occurring in weedy, grassy, and herbaceous vegetation of many different kinds. It is especially common along roadsides and in other "border" situations. It song can be heard continuously mile after mile along roadsides, both day and night.

Walker (1905, 6) found this species adult in Ontario between the end of July and the beginning of October in upland fields as well as low meadows. Blatchley (1920, 6) says it becomes adult in central Indiana about July 10, and is found in upland localities, along fencerows, and in clover and timothy meadows, and on ironweed in bluegrass pastures. Hubbell (1922, 6) found adults from August 3 to September 9 in Michigan, in sedge and lizard's tail marshes, tall grass and weeds along roadsides and fences, in thickets along the margins of woods, fields grown up with bushes and shrubbery, wheat and clover fields, tall grass and dewberry vines in dry, sandy fields and pastures, among grapevines and clumps of bunch grass on dune slopes. Hebard (1938, 6) says adults appear in mid-July in Pennsylvania in the open, particularly on tall weeds. Cantrall (1943, 6) found adults from July 24 to October 14 in semi-permanent marshes and later in the season erratically in the "mixed-grass herbaceous habitat."

Singing Behavior

This species sings both day and night, but sometimes at night it leaves out the ticking phase of its song, as has also been noticed in *O. gladiator*. Males caged together often produce only this ticking phase, or produce more ticks than usual.

Singing males are usually perched from 2 to 5 feet above the ground, most often in a vertical, head-up position. Singing individuals seem at times to be alternating songs, at other times the songs of neighboring individuals are synchronised or nearly so for long periods of time, and at still other times two males will be singing near each other with neither alternation nor synchronisation apparent. Males in the field remain on one weed, or sing from one weed, or one small area, for long periods of time, probably throughout their adult life if undisturbed.

Song Records

*Dyar Co., Tenn. (Thomas Walker, coll.) (1) 23 Sept. 1955, 74° F., (2) 25 Sept. 1955, 80° F.

*Piatt Co., Ill. (Sangamon Twp.) 4 Sept. 1955, 60° F.

*Franklin Co., O., 8 Aug. 1954, 85° F., 2 min., 40 sec.

*Franklin Co. O. (University Woods) 28 July 1954, 74° F., 2 min. 28 sec.

*Franklin Co. O. (Clinton Twp.) (1) 29 July 1954, 96° F., 85 sec., (2) 24 Sept. 1954, 65° F., 83 sec., (3) 28 July 1954, 70° F., 2 min., 50 sec.

Song Description and Analysis

From 6 to 34 double-pulse ticks occur between the buzzes in this song. They are produced somewhat irregularly, often in groups of 3 or 4 at 8-9 per second (80° F.), and may or may not be attached to the front of a buzz. Often a few are delivered at the end of each buzz. The buzzes have a pulse rate of 45-140 per second (70-100° F.) and last 4-8 seconds. They characteristically increase in intensity and then end abruptly, this character distinguishing the song to the ear from the similar songs of gladiator, pulchellum, and agile. The phrases are delivered at rates of from 6 to 8 per minute. At night the ticks are often reduced in number or completely absent.

This song has been described by a number of authors, including Scudder (1893, 6), Cantrall (1943, 6), Pierce (1948, 26), and Pielemeier (1945, 6). These descriptions agree essentially with that given here. Pierce gives average pulse rates of 51 and 66 per second for specimens with normal and clipped wings, respectively (no temperatures given), and he says 7-42 ticks occur between buzzes. Pielemeier found peaks in the frequency spectrum of the sound of this species at 60 cps. (26 decibels at one foot), 7.1 kps. (36 db. at one foot), 14.2 kps. (70 db. at one foot), and 18-20 kps. (69 db. at one foot). He recorded a wingstroke rate of 60 per second, determined with a stroboscope (no temperature given).

Orchelimum gladiator Bruner

Gladiator Meadow Grasshopper

Distribution

This is a northern species, according to Rehn and Hebard (1915, 6), "covering the grassland areas and bottom lands of the northern United States and southern Canada." They give the southern limits of distribution as northern California, south-central Montana, south-central Nebraska, Northeastern Kansas, Tennessee, southern New Jersey, and southwestern Connecticut. Hebard (1938, 6) gives Champaign as a southern limit in Illinois. In the present study it has been encountered in Plain Township, Franklin County, Ohio, in two different marshy areas, and in Specht Marsh in Carroll County, Ohio. All three colonies were located in dense cattail marshes.

In Franklin County, this species is the first meadow grasshopper to mature, beginning to sing in early July, and was singing in large numbers on July 11 in both 1954 and 1955. It is gone before September 1 in this area, and was last collected on August 14 in Carroll County.

Blatchley (1920, 6) found this species in damp prairies, meadows, and marshes in northern Indiana, maturing about July 10. Hubbell (1922,

6) found adults from July 3 to July 22 in Michigan in marshes and wet meadows and in similar situations to those in which vulgare occurs later in the season. He says gladiator seems to have the same seasonal relationship to vulgare that Arphia sulphurea has to A. xanthoptera, appearing early and being replaced during the latter part of the season by the other species. Hebard (1938, 6) says adults appear early in July in Pennsylvania and frequent wet, grassy areas and bogs. Cantrall (1943, 6) found adults from July 3 to September 4 in semi-permanent and permanent marshes. On the George Reserve, Michigan, he says it has the same relationship to vulgare as Pardalophora apiculata has to P. haldemanni.

Singing Behavior

This species sings both day and night, and as with vulgare, often leaves out the ticking part of its song at night, and when several males are caged together a disproportionate amount of ticking occurs. These observations would lead one to the suggestion that the ticking part of the song is a result of a visual stimulus, and that it could feasibly be the part of the song chiefly involved in the spacing of the males. This could help explain the maintenance of such 2-part songs.

Song Records

*Franklin Co., O. (Plain Twp.) 12 July 1954, 85° F., 5 min. (2) 11 July 1955, 89° F., 80 sec. (3) 40 sec. (4) 90 sec. (5) 70 sec. (6) 100 sec.

*Carroll Co., O. (Specht Marsh) 14 Aug. 1954, 65° F. (night), 11 songs in 1 min., 50 sec.

Song Description and Analysis

Three to thirteen single-pulse ticks per buzz occur in the song of this species, produced at about 5 per second (89° F.). The buzzes last 1.5-3.5 seconds, and have a pulse rate of about 50 per second. The song rate is about one every 3-4 seconds.

Cantrall (1943, 6) gives 0-8 ticks per buzz in regular singing and mentions the absence of ticks in undisturbed singing and at night, and the increase in number of ticks in the songs of disturbed males. He gives the buzz length as 1-4 seconds.

Pierce (1948, 26) found very few ticks in a recorded series of songs of this species, which may have been produced at night. He says the pulse rate is 38 per second, the toothstrike rate 3.5 per second, and the principal frequency 16 kps.

Orchelimum silvaticum McNeill

The Long-Spurred Meadow Grasshopper

Distribution

This is a southwestern species, ranging from west-central Texas northeast through Arkansas, Kansas, South Dakota, and Iowa east to central Ohio. In Illinois, Indiana, and Ohio, its northern limits are Charleston (Hebard, 1934, 26), and Columbus (Ohio), respectively.

In this study adults of this species have been encountered in

Franklin, Champaign, and Hocking Counties, Ohio, between July 29 and September 21, in tall weeds, shrubbery, and small trees. At the Ohio State University woodlot it occurs in small trees in sunny, open areas inside the forest and along its border. On occasion, individuals have been found on small weeds, such as ragweed, within a foot of the ground, and at the other extreme, 15-20 feet high in trees. Hebard (1938, 6), apparently citing records of E. S. Thomas (Ohio), says this species appears adult in July and prefers the undergrowth along forest borders and in open woodland.

Singing Behavior

This species sings both day and night and the males are sedentary, individuals on the Ohio State University Campus having been observed in the same trees over a period of two weeks. On one occasion a male was watched singing steadily while he ate a small bee which he had apparently captured from the blossom where he was perched. The song of this male was heard from this bush almost daily for about 3 weeks.

No observations on synchronization, alternation, or any other song (except the calling song) have been made.

Song Records

*Franklin Co., O. (OSU Campus) 29 July 1954, 96° F. (10 feet up in cottonwood) 12 songs in 2 min., 5 sec.

*Franklin Co., O. (Clinton Twp.) 23 Aug. 1954, 71° F. (2 feet up on horseweed) 5 songs in 45 sec.

*Hocking Co., O. (Neotoma) 7 Sept. 1954, 85° F. (8 feet up in pine) 10 complete, 26 plus incomplete songs in 3 min., 18 sec.

*Franklin Co., Ky. (Thomas Walker, coll.) 15 July 1955, 84° F. (wooded pasture) 13 songs in 2 min., 55 sec.

Song Description and Analysis

The song of this species is a continuous repeating, at 6 per minute, of a 2-part phrase. This phrase is a buzz with the pulses in the first third or half delivered at a slower rate than those in the last part. These are probably homologous with the ticks in other meadow grasshopper songs. The whole phrase lasts 3-4 seconds at 70° F. In the songs of the 4 individuals recorded, the number of pulses in the first part of the phrase varied from 4 to 26, and were delivered at 12-20 per second. The number of pulses in the last part of the phrase varied from 15 to 136 (usually 50-130), and were delivered at from 27 to 40 per second.

Orchelimum nigripes Scudder

The Black-Legged Meadow Grasshopper

Distribution

This species has a central distribution, extending from Ontario and Minnesota south to Texas and Louisiana. In Tennessee it is known from Clarksville (Rehn and Hebard, 1915, 6), and it occurs all over Illinois, Indiana, and Ohio. Westward it extends to western Nebraska and Colorado. During the present study it has been encountered in Piatt and DuPage Counties, Illinois, Lawrence County, Kentucky (Thomas Walker), and Erie, Licking, Pickaway, Carroll, and Franklin Counties, Ohio. At Columbus, Ohio, it can be heard from late July until frost. It is found in grassy and weedy areas of many descriptions across Ohio, Indiana, and Illinois, but seems to occur at its greatest densities in marshy and swampy areas.

Blatchley (1920, 6) says this species reaches maturity about July 20 in Indiana, and is found "by hundreds about the margins of every lake, pond, and marsh in the state." Hubbell (1922, 6) found adults between August 30 and September 9 in Michigan, on buttonbush shrubs in swampy thickets, in the branches of tall shrubbery, and on hanging grapevines in the margins of woods, in hawthorn, elm, box elder, and other trees, in open portions of the flood-plain forest, often as much as 25 or 30 feet from the ground, from willows bordering a dune pond, tall grass clumps and weeds in bunch grass among dunes, and in a lake shore reed marsh. Hebard (1938, 6) says adults appear in late July in Pennsylvania, and are usually present in great numbers in vegetation bordering water, and he cites Ohio records by E. S. Thomas. Cantrall (1943, 6) found adults from July 18 to September 21 only on dogwoods and buttonbush in the "wet shrub-zone habitat" on the George Reserve, Michigan.

<u>Singing Behavior</u>

This species sings both day and night, and the singing males are usually perched 3-5 feet above the ground on herbaceous vegetation, but occasionally in low, wet timber or swamp forest associations, it is heard from high in trees, as indicated above (Hubbell). A male located on a small weed along a path taken 4 times daily for a period of several weeks in August and September was heard continuously during this period, and always from the same plant.

Neighboring males of this species alternate their songs in rapid succession for long periods of time. This was observed both in the field, and in males caged together in the laboratory for about two weeks. This continuous alternation of songs was observed to last for over a half hour one day without a break.

Cantrall (1943, 6) indicates that this species does not normally sing after dark. This at variance with observations made in the present study. I have recorded it at all times of the night, as late as 3 A. M. Allard (1910d, 6) also says it sings both day and night.

Song Records

*Piatt Co., Ill. (Sangamon Twp.) 5 Sept. 1955, 59° F., 6 songs in 56 sec. (not regular singing), 2-4 single-pulse ticks at 4 per sec., 36-44 pulses per buzz at 16 per sec.

*Madison Co., O. (Madison Lake) 27 July 1954, 85° F., 43 songs in 2 min., 45 sec. (disturbed singing — as many as 38 ticks between buzzes), 12 ticks per sec., 3/4-1-second buzzes with 88 pulses per sec.

*Carroll Co., O. (Specht Marsh) 14 Aug. 1954, 85° F. (1) 9 songs in 48 sec. (not regular singing), 3-7 ticks per buzz at 16 per sec., 3/4-1-second buzzes with 66 pulses per sec. (2) 35 songs in one min., 45 sec., 2-5 ticks at 10 per sec., 3/4-1-second buzzes with 85-90 pulses per sec.

*Franklin Co., O. (Clinton Twp.) 24 Sept. 1954, 65° F., 8 songs in 60 sec. (not regular singing), 3-8 ticks at 8 per sec., 37-71 pulses per buzz at 16-20 per sec.

*Erie Co., O. (Cedar Point) 26 July 1955, 78° F., 4 songs in 30 sec., 2 pulses (ticks) at 5 per sec., 3/4-1-second buzzes with 40 pulses per sec.

*DuPage Co., Ill. (Bemis Woods) 18 Aug. 1954, 70° F., 5 songs in 23 sec., 2-4 ticks per buzz at 8 per sec., 1-13/4-second buzzes with 16 pulses per sec.

Song Description and Analysis

This song is a quick repeating of short, rather soft phrases (3-4 in 5 seconds in regular singing at 80-85° F.). The ticks are single-pulse and are rapidly delivered and attached to the front of the short buzzes. The most common number of ticks, 2-4, but disturbed individuals sing irregularly and may produce many ticks between buzzes in irregular groups of 2-5.

Cantrall (1943, 6) says there are invariably 2 ticks in the song of this species on the George Reserve, Michigan, and that the song rate varies from 16 to 28 in 30 seconds (no temperature given). Song descriptions given by Allard (1910d, 6, Thompson's Mills, Georgia) and Walker (1905, 6, Ontario) do not disagree with that given here.

Orchelimum minor Bruner

The Pine Tree Meadow Grasshopper

Distribution

This is a southeastern species, extending from New Jersey south to southern Georgia (Rehn and Hebard, 1915, 6), and west to Lenoir, North Carolina and Hocking County, Ohio (present study). In this study it was encountered on September 3-4, 1954, in Hocking County, Ohio, and on August 8-11, 1955, at Lenoir and Raleigh, North Carolina. Fulton (1951, 6) gives song records for this species between early August and late October at Raleigh, North Carolina, and says it sings from the tops of pines day and night (1932, 6). Hebard (1938, 6) says adults appear early in August in Pennsylvania, and are arboreal and peculiar to pines. Fox (1917, 6) found adults between September 19 and October 13 in Virginia, in Pinus virginiana and P. taeda.

Singing Behavior

This species sings day and night, and is one of the few known arboreal species that does so. In Hocking County, Ohio, it was rarely found below 10-15 feet above the ground, and was often considerably higher. Caged males sang readily in the laboratory, but no synchronization or alternation was evident in their singing.

Song Records

*Hocking Co., O. (Neotoma) 3 Sept. 1954 (1) 73° F., 51 songs in 55 sec., 18.4 pulses per sec., 16-25 pulses per buzz (average, 22.1), (2) 80° F., 127 songs in 140 sec., 17.2 pulses per sec., 6-18 pulses per buzz (average, 13.3), (3) 48 songs in 50 sec., 21.6 pulses per sec., 6-16 pulses per buzz (average, 12.9).

Lenoir, N. C., 8 Aug. 1955; Raleigh, N. C., 9-11 Aug. 1955.

Song Description and Analysis

This song is a continuous repeating of a soft, fluttery buzz lasting ½-1 second, at a rate of about one per second. It is audible several yards away. As shown above, the pulse rate in these buzzes is from about 17 to 22 per second (73-85° F.). The first individual above was recorded in the field, the other two in the laboratory. It is noteworthy that the busses of the individual recorded in the field averaged considerably longer than those recorded in the laboratory. This is typical of the kind of distortion one may obtain in laboratory recordings of insect songs. Presumably a disturbed singer shortens his busses.

Although the buss of this species sounds uniform to the ear, it begins with a slightly detached pulse (Plate XLIII), as do the busses of several species of Orchelimum. This is apparently the only part of the ticking phase retained in this song.

The Orchelimum concinnum Complex

Rehn and Hebard (1915, 6) and other authors have considered Orchelimum campestre Blatchley and O. delicatum Bruner as synonyms of O. concinnum Scudder. Blatchley (1920, 6) considers the 3 forms as subspecies of concinnum. Thomas (1951, 6) considered the three as distinct species "since they exist together in a number of places without evident intergradation." Specimens of all three species have been collected and recorded during the present study, and subsequently identified by Dr. Thomas.

O. delicatum was collected and recorded along Lake Erie at Cedar Point, Ohio. O. campestre was collected and recorded from Cedar Swamp in Champaign County, Ohio, DuPage County, Illinois, and Franklin County, Kentucky (Thomas Walker, coll.). O. concinnum was collected and recorded from Cedar Swamp, Champaign County, Ohio. In no case were all 3 forms found together. Concinnum and campestre both occur at Cedar

Swamp, but in different parts of the swamp.

The specimens identified by Dr. Thomas as campestre had a song quite distinct from those of the other two species, which are very similar, but can be separated by Vibragrams, at least in the few specimens recorded. Concinnum is characterized by a red stripe down the center of the face, while neither campestre, with a quite different song, nor delicatum, with a similar song, has any markings other than green on the face. Both adults and immatures of concinnum collected at Cedar Swamp on July 30, 1955, had red stripes on the face, although Hebard (1934, 26) states that a specimen which he reared had an immaculate face until it molted to adulthood, whereupon it developed the heavy red-brown stripe characteristic of concinnum. In 1915, 6, Rehn and Hebard say that in the eastern coastal region two color forms are present in the young, one which has a striped face and one which has an unbarred face, "but within a few days after becoming adult, as the chitin thoroughly hardens the stripe develops and becomes as prominent as in the other type. This was ascertained by keeping specimens under observation from the immature stages to that of thoroughly hardened adults. It is very probable that green face adult specimens from New Jersey were taken before they had fully acquired their permanent adult coloration."

Dr. E. S. Thomas distinguishes the males of these three forms on the basis of cercal characters, and in the present paper they will be treated as distinct species.

Thomas (1951, 6) believes that these three species diverged as a result of temporary isolation during the Pleistocene, with campestre a middle western endemic surviving glaciation in refugia not far from the ice front, concinnum spreading eastward into the Great Lakes Region from the Atlantic coast in early post-Wisconsin times, and delicatum, the western form, moving eastward during the Xerothermic period in grassy swales. Campestre is known from Wisconsin, Michigan, Illinois, Indiana, Ohio, Kentucky, and Tennessee; concinnum occurs in the northern parts of Ohio, Indiana, and Illinois, in Michigan, and elsewhere only along the Atlantic coast from Maine to North Carolina; delicatum extends from western New York westward to Kansas, Nebraska, and the Dakotas, occurring in Michigan, northern Ohio, Indiana, and Illinois.

Orchelimum concinnum Scudder

The Dusky-Faced Meadow Grasshopper

This species was observed in the field only once, in a small colony in Cedar Swamp in Champaign County, Ohio. The colony was located about dusk on July 1, 1955. The males were singing from perches 1-3 feet above the ground in sedges in a wet areas along a stream bank. Only a few individuals were singing at a time, and their combined sound did not attract my attention until I was only a few yards from the colony. In the laboratory these males sang readily, and lived until around mid-August on ground dogfood.

Song Records

*Champaign Co., O. (Cedar Swamp) 3 Aug. 1954 (lab) 91° F., 4 specimens, about 12 min.

Song Description and Analysis

This song contains 1-3, single-pulse ticks per buzz at 2 per second. The buzzes last 1-2 seconds and have a pulse rate of about 30-35 per second (Plate L). The song rate in steady singing is about 4 in 10 seconds.

Fulton (1932, 6) says 1-5 ticks occur at a rate of 2-3 per second with buzzes lasting ½-1 second. Pierce (1948, 26) gives 6-9 ticks at 3 per second, and buzzes lasting 2-3 seconds. He gives the toothstrike rate as 250, and the principal frequency 20.3 kps. He gives a pulse rate of 28 per second (temperature not mentioned).

Orchelimum delicatum Bruner

The Delicate Meadow Grasshopper

This species was located in a dense cattail marsh along Lake Erie near Cedar Point on July 27, 1955. Several adults were captured along with adults of O. volantum and C. attenuatus. They were not heard singing, probably because of their soft song, and the fact that volantum was singing loudly in the same area. Males and females both were obtained by sweeping 4-5 feet from the ground in the cattails.

Hubbell (1922, 6) found adults from July 21 to August 15 in North Dakota, in thick patches of sedge on the shores of Devil's Lake and in honeysuckle in a bare pasture near a woods edge, and in a dry coulee in tall grass a half mile from the lake. Blatchley (1920, 6) found adults on July 30 and August 20 in lowland meadows near large lakes in Indiana.

Song Records

*Erie Co., O. (Cedar Point) August 1954 (lab) 90° F., 3 specimens, about 7 min., 30 sec.

Song Description and Analysis

This song contains 2-4 ticks per buzz in steady singing, with several sometimes following the buzz in the songs of slightly disturbed males. The ticks are double-pulse, and are produced at a rate of 2-4 per second. The buzzes last about 1 second and have a pulse rate of about 40 per second (Plate L). The song rate in steady singing is 5-6 in 10 seconds.

Orchelimum campestre Blatchley

Blatchley's Meadow Grasshopper

This species was collected between August 3, 1955, (Cedar Swamp) and September 16, 1955, (DuPage Co., Ill.). Aside from these two occasions it was observed only twice, at Cedar Swamp on August 24, 1954, and by Thomas Walker in Franklin Co., Ky., on July 15, 1955. In DuPage Co., Ill., it was found along the border of a large permanent marsh; in Cedar Swamp it occurs in the sedge meadow, the singing males 2-3 feet above the ground. Singing was noticed both day and night in the field, and caged males sang readily in the laboratory.

Blatchley (1920, 6) records this species in Indiana from upland bluegrass pastures and the tall grasses of the drier prairies and says it is seldom, if ever, found about the lakes and marshes in company with typical concinnum. Cantrall (1943, 6) found adults from August 5 to October 3 on lake margins in Michigan.

Song Records

*Champaign Co., O. (Cedar Swamp) (1) 24 Aug. 1954, 73° F., 3 min., 30 sec. (2) 3 Aug. 1955, 91° F. (lab), 2 min., 30 sec., 2 specimens, (3) 85° F., about 5 min.

*DuPage Co., Ill., 16 Sept. 1955, 76° F., 1 min., 55 sec.

*Franklin Co., Ky., 15 July 1955, 84° F. (lab), 7 min.

Song Description and Analysis

The song of this species, as with most other meadow grasshoppers, consists of both short "ticks", produced by one wingstroke, and longer buzzes produced by prolonged vibration of the wings. However, its song is unique in that the zips are often omitted, and the buzzes may last up to several minutes without pause. The song is difficult to characterize because of the amount of variation involved. Sometimes an individual will sing along, very much like either concinnum or delicatum, then he will produce a continuous buzz lasting several minutes. Several meadow grasshoppers produce continuous buzzes, but no other species does both kinds of singing. The number of ticks this species produces at a time may vary from 1 to 150 or more, and the buzzes may last from 1 to 2 seconds up to 2 to 3 minutes. The single-pulse ticks are produced at 2 per second at 76° F., and the pulse rate in the buzz is about 20 per second (Plate L). The song is rather soft, but can be heard 20-30 yards.

Cantrall (1943, 6, George Reserve, Michigan) says, "The complete song of campestre is audible for about thirty feet. Beyond that distance the introductory notes cannot be heard. In its entirety, it may be written as 'zick-tick-tick-z.z.z.z.z.z.z.z.z.' The first note or 'zick' is always struck once and the 'tick's' are sounded from two to seven times. The remainder of the song is steady and buzzing in quality and lacks the 'zing' and sharpness of the notes of O. gladiator. This part may be sounded without interruption for from four to forty-eight seconds."

Apparently the only difference between Cantrall's description and that given above is that his extremes are not as great. I have not been able to detect the distinctive "zick" or introductory note described by Cantrall.

Orchelimum volantum McNeill
The Nimble Meadow Grasshopper

Distribution

This species is central in distribution, extending from south-central Ontario to south-central Ohio, its southern limit extending from Pickaway County, Ohio (present study), west across Vigo County, Indiana (Blatchley, 1920, 6), and Peoria, Illinois (Hebard, 1934, 26), to eastern Nebraska.

In the present study this species has been encountered in a dense cattail marsh in Erie County, Ohio, on July 27, 1955, and in a Calamus swamp in Pickaway County, Ohio, west of Circleville on September 26,

1954. In both locations it occurred in company with Conocephalus attenuatus, and in the Erie County marsh, also with O. delicatum. In Erie County its song could be heard continuously in the dense cattail marshes along the edge of Lake Erie. In Pickaway County, it was found in a dense growth of Spanish needle and smartweed (Polygonum).

Walker (1905, 6) found volantum abundant among the rushes and Sagittaria growing in open marshes bordering streams in southern Ontario. Blatchley (1920, 6) found adults most abundantly during August and September on the leaves and stems of Polygonum amphibium L. around the margins of the larger ponds and lakes in Indiana. Hebard (1938, 6) says this species lives only on plants which grow out of water, and states that it is usually possible to obtain specimens only from a boat, or by wading in waist-deep water. Hebard says adults appear in mid-July in Pennsylvania, and that the species is "essentially aquatic and fairly frequent on Spatterdock, Nympha adrena, which grows in water."

Singing Behavior

This species sings by day, and probably also at night, though its habitat has not been visited at night during this study. The singing males are usually 4-7 feet above the ground, and are probably the most agile and difficult to capture of all the Orchelimum species treated here. Like the smaller species with which it is often found (C. attenuatus), a disturbed individual will often jump repeatedly until it has travelled completely out of sight in the vegetation. When approached, a singing male stops his noise, and in the manner typical of the meadow grasshoppers flattens himself against the stem upon which he is perched and proceeds to edge around it as the observer approaches, always keeping the stem between himself and the observer. During this behavior, the antennae are usually extended lengthwise up the stem, and are thus also rendered nearly invisible. However, at times these appear, waving, and often this is the only way an individual can be spotted.

A caged male sang readily in the laboratory. No synchronization or alternation of songs has been noticed, either in the field or in the laboratory. Two caged males sang during a scuffle on one occasion.

Song Records

*Pickaway Co., O. (one mile west of Circleville) 26 Sept. 1954, 84° F., 2 individuals, about 5 min.

Song Description and Analysis

This song is a continuous, more or less regular repetition of a loud, coarse phrase lasting a little less than a second, at rates of 1 in 2-4 seconds. The phrase increases in intensity for about a third of a second, then dies out towards its end in both intensity and speed of pulsation (Plate XLIII). The pulse rate in the first part of the phrase is about 65 per second and this gradually slows until the last few pulses are delivered at about 30 per second.

The song is noticeable several yards away because of the "suddenness" of the phrase.

Orchelimum pulchellum Davis

The Handsome Meadow Grasshopper

Distribution

This is a southeastern species, extending north along the coast to north central New Jersey (Rehn and Hebard, 1915, 6, under *laticauda* Redtenbacher), and southeastern Pennsylvania (Hebard, 1938, 6), west to New Orleans, Louisiana, Thompson's Mills, Georgia (Rehn and Hebard, 1915, 6), and Raleigh, North Carolina (Fulton, 1951, 6). In the present study it was encountered 12 miles south of Raleigh, North Carolina, in the weeds around a farm pond on August 8, 1955.

Fulton (1951, 6) gives the seasonal song period of this species at Raleigh as from mid-July to November 1. In 1932, 6, he says the habitat is along the borders of streams and ponds. Fox (1917, 6) found adults from August 8 to October 13 in tidal and fresh water marshes and pond borders in Virginia, with the males, at least, spreading in small numbers to upland districts where it was taken in dense millet and ragweed. He says it appears to have a strong preference for woodland habitats. Hebard (1938, 6) says adults appear in early August in southeastern Pennsylvania, in high swamp and marsh vegetation.

Singing Behavior

The only specimen I have heard singing was located about 3 feet off the ground in weeds and was singing at night. Later this specimen sang in daylight in a cage.

Song Record

*Raleigh, N. C. (McCuller's Pond) 15 Aug. 1955 (lab), 85° F., 24 songs in 1 min., 27 sec. (steady singing).

Song Description and Analysis

This song contains 1-4 (usually 1) single-pulse ticks per buzz, at rates of from 5 to 12 per second. The buzzes last about 3/4 second and have a pulse rate of about 35 per second. As shown above, the song rate in steady singing is about 1 every 3-4 seconds.

Davis (1909, 6) says the song of this species has 3 zips (ticks) for every buzz and is "quite a distinguishable song from that of vulgare." Fulton (1932, 6) says 4-6 ticks occur at a rate of 6 per second, with the buzz lasting ½-3 seconds and rather weak and fluttering.

Conocephalus fasciatus fasciatus (DeGeer)

The Slender Meadow Grasshopper

Distribution

This species occurs all over the United States, north into Canada, and is also known from Bermuda (Rehn and Hebard, 1915, 6). In the region of Pacific drainage the typical subspecies is replaced by fasciatus vicinus (Morse).

In the present study, fasciatus has been encountered in DuPage, Piatt, Jackson, and Alexander Counties, Illinois, Champaign, Delaware, Franklin, Licking, Pickaway, Madison, Hocking, and Adams Counties, Ohio, and Wake County, North Carolina.

This little insect occurs in a wide variety of grassy and weedy situations, but is most abundant in damp areas. In Adams County, Ohio, it was found in large numbers in a closely grazed lowland bluegrass pasture along a creek, in company with Nemobius socius. At Cedar Swamp it was found on the marshy bank of a stream. In Piatt County, Illinois, Franklin County, Ohio, and Bourbon County, Kentucky (Thomas Walker, coll.), it was found in well-drained bluegrass pastures, and in Wake County, North Carolina, it was collected in a stubble field.

At Columbus, Ohio, this species was first taken adult on July 10, 1954, but at Carbondale and Cairo, Illinois, it was heard and collected June 15-16, 1955. Adults have been taken as late as September 20 at Columbus, but probably do not disappear until frost.

Fox (1917, 6) found adults between June 15 and November 5 in Virginia, and says it may be double-brooded there. He says it occurs generally in moist or wet open grassy fields and pastures, and largely avoids woody locations, being more restricted to humid areas in the Piedmont and Appalachian mountain sections than in the Coastal Plain. Blatchley (1920, 6) found adults on July 5, and records this species in Indiana as abundant in timothy and clover meadows and especially about small streams in lowland bluegrass pastures. Hubbell (1922a, 6) found adults from July 4 to September 9 in Michigan, in grassy fields and pastures, moist meadows, weed thickets, and marshes, more numerous in moist than in dry habitats. Hubbell (1922b, 6) found adults between July 19 and August 31 in North Dakota, on dry flats around lake shores, in grass and sedge marshes, moist meadows, brushy fields and pastures, dry grassland, and cultivated fields. Hebard (1938, 6) says adults appear early in July in Pennsylvania, in the open in grasses. Cantrall (1943, 6) found adults from July 25 until frost in semi-permanent and permanent marshes on the George Reserve, Michigan, and elsewhere in Michigan in damp situations which maintain growths of lush and rank-growing grasses.

Singing Behavior

This species sings day and night, and is almost invariably within 2 feet of the ground, usually perched vertically, head-up or head-down. Often it is found in closely grazed pastures or well-kept lawns, practically on the ground.

Song Records

*Adams Co., O. (Lynx) 10 July 1954, 80° F., 7-28 ticks per buzz at 5 per second; buzzes lasting 2-20 sec., usually about 5-10; 26 songs in 5 min., 5 sec.

*Franklin Co., O. (Clinton Twp.) 24 July 1954, 96° F., 22-28 ticks per buzz at 12 per sec.; buzzes lasting 2-15 sec.; 1 min., 45 sec at 1 song per 10 sec.

*Champaign Co., O. (Cedar Swamp) 24 Aug. 1954, 84° F., 3-7 ticks per buzz; buzzes lasting 2-3 sec.; 1 min., 15 sec. at 1 song per 9 sec.

*Madison Co. O. (Madison Lake) 31 July 1954, 85° F., 8 phrases in 45 sec.; 4-12 ticks per buzz at 4 per sec.; buzzes lasting 2-4 sec.; 2 min., 50 sec.

*Bourbon Co., Ky. (Thomas Walker, coll.) 10 July 1955, 84° F., 8-22 ticks per buzz at 4-6 per sec.; buzzes lasting 1-5 sec. (usually 3); 1 min., 50 sec, 15 songs.

*Wake Co., N. C. (McCuller's Pond) 8 Aug. 1955, 76° F., 24 ticks and 1 buzz requiring 20 sec.

Song Description and Analysis

This is a very soft song, audible only a few feet away under favorable conditions, and it is usually not detected unless one is already kneeling or otherwise down near the ground. At night it is completely obscured by other insect sounds. As with most songs of Conocephalinae it consists of an alternation of ticks (single wingstrokes) and buzzes (series of wingstrokes). These occur at the rates and numbers given in the song records above. The pulse rate in the buzz is about 35 per second at 80° F. The song is separable from that of *brevipennis*, the only *Conocephalus* song treated here which resembles it, by the larger number of ticks.

Allard (1911a, 6) gives 1-14 ticks per buzz for this species, with buzzes lasting 5-20 seconds, and he says one series of 71 ticks occurred with no buzz. Walker (1904, 5) says the song of *fasciatus* in Ontario sounds like a faint echo of *vulgare*, but the "sip" (tick) is emitted only once or twice at a time and at shorter intervals. This sounds more like the song of *brevipennis*. Cantrall (1943, 6) says from one to many ticks may be produced, and they may be produced in long series for 10-15 seconds, or given indiscriminately before or after buzzes. He gives buzz lengths for one male, at 88° F., of from 1/4 to 4 seconds.

Pielemeier (1945, 6) found peaks in the frequency spectrum of this species at 8.3 kps. (61 db. at one foot), 17.4 kps. (35 db. at one foot), and 28 kps. (48 db. at one foot). He calculated the wingstroke rate at 80 per second (no temperature given).

Pierce (1948, 26) says 2-26 ticks occur between buzzes which last

2-5 seconds and have a pulse rate of 37-53 per second. He gives a toothstrike rate of 288 per second and says the principal frequency of the sound is 40 kps., with a weaker component at 16.3 kps.

Conocephalus brevipennis (Scudder)

The Short-Winged Meadow Grasshopper

Distribution

This species is found from Canada to Florida on the east coast and west to Minnesota, Nebraska, and Texas (Rehn and Hebard, 1915, 6). In the present study it has been encountered in Franklin, Licking, and Hocking Counties, Ohio, from September 1 to September 20. Adults undoubtedly appear earlier than this. It has been found in grassy fields, pastures, and roadsides, on fine-stemmed plants such as bluegrass, timothy, foxtail, etc.

Fox (1917, 6) found this species adult between August 18 and November 4 in Virginia, in moist and somewhat humid situations in pastures and meadows, spreading into the relatively dry grassy or shrubby undergrowth of open deciduous woods of mountain summits. In the Piedmont region he found it largely confined to low, humid marshes, ditches, springheads, drains, etc., or the denser undergrowth of woods. Blatchley (1920, 6) says this species reaches maturity in Indiana about August 10 and occurs in the same habitats as C. fasciatus. Hubbell (1922a, 6) found adults between August 3 and September 7 in Michigan, abundant, and the only Conocephalus, in thick rank growth of nettles, ironweed, low bushes, and vines in a lowland thicket, and otherwise in the same situations as fasciatus. Fulton (1932, 6) says this species sings in wet places, either in woods or open marsh in North Carolina. In 1951, 6, he gives its seasonal song period at Raleigh as about August 10 to November 1. Hebard (1938, 6) says adults appear early in August in Pennsylvania, in the open, but preferring a somewhat shaded environment. Cantrall (1943, 6) found adults from August 1 to Octuber 14 on the George Reserve, Michigan, in semi-permanent and permanent marshes, and erratic in mixed grass-herbaceous, shady oak-hickory, and bog habitats, not over 100 feet from marshes.

Singing Behavior

This species sings day and night, and readily in the laboratory. The singing males are usually within 2 feet of the ground, often in the same areas as fasciatus and strictus, and perched in the typical vertical position of singing Conocephalinae.

Song Records

*Licking Co., O. (Buckeye Lake) 10 Sept. 1954, 80-85° F., 2 min., 15 sec., 51 songs, 2-4 ticks per buzz.

*Hocking Co., O. (Laurel Twp.) 17 Sept. 1954, 85° F., 2 min., 5 sec., 76 songs, 1-5 ticks per buzz at a rate of 2.6 per sec.

*Franklin Co., O. (Clinton Twp.) Sept. 1954, 80-85° F., 73 sec., about 12 songs per min., 3-7 ticks per buzz.

Song Description and Analysis

This is a soft sound, as are all the Conocephalus songs, and is audible only a few feet away. It consists of a continuous repetition of short busses lasting about one second each and separated by 1-7, but nearly always 2 or 3, ticks at a rate of about 2-3 per second. The number of ticks shown above includes the one which is almost attached to the front of each buzz, and practically inaudible in the song at normal speed. In other words, if one counts the number of ticks between buzzes in a song heard in the field and consistently gets 2-3, this is equivalent to 3-4 as given above. The pulse rate in the buzz is 50-60 per second at 85° F.

Allard (1911a, 6) says that 1-2 ticks precede 1, 2, or even 3 buzzes in the song of this species in New England. Cantrall (1943, 6) says this description fits the songs of Michigan specimens, and Fulton (1932, 6) describes the song similarly for North Carolina. Walker (1904, 6) says 1-2 ticks are produced, at a rate of about 1 per second, and that otherwise the song is very much like that of _fasciatus_. Pierce (1948, 26) found 1-2 ticks per buzz, with the pulse rate in the buzz 42-55 per second, the toothstrike rate 700 per second, and the principal frequency 47 kps., with a secondary frequency of 34 kps. He does not mention the production of 2-3 buzzes for each set of ticks, which seems to be the chief difference between the descriptions of other authors and that given here. In only one instance in the song records given above, do two buzzes occur without ticks between them.

Conocephalus _nemoralis_ (Scudder)

The Woodland Meadow Grasshopper

Distribution

According to Rehn and Hebard (1915, 6), this species is known from New Jersey to North Carolina and west to Kansas, Nebraska, and Wisconsin. In the Present study it has been encountered in Hocking, Franklin, Licking, and Pickaway Counties, Ohio, and Piatt County, Illinois. At Columbus, Ohio, it has been heard between August 19 and October 2. It occurs in brushy areas along forest borders, in the undergrowth of open forests, in brushy fencerows, and in brush-filled pastures. On the Ohio State University Campus it is commonly heard in shrubbery and small trees.

Fox (1917, 6) found adults on October 10 and 31 at Charlottesville, Virginia, and on Carter Mountain. Blatchley (1920, 6) says it reaches maturity about August 1 in Indiana, and is found along the borders of dry, upland woods, in fencerows and along roadsides on shrubs, blackberry bushes, or coarse weeds. Hubbell (1922a, 6) found adults in Michigan on September 9 among clumps of bunch grass on the inland side of sand dunes near the edge of an open oak woods and in the margins of woods. Hebard (1938, 6) says adults appear early in August in Pennsylvania, and the species is "sylvan and very local, but when present usually in moderate numbers in woodland grasses."

Singing Behavior

This species sings night and day, perched from a foot or so above the ground up to 5-6 feet. The males are very persistent singers, not easily disturbed, and sometimes will only pause an instant even when forced to jump, beginning to sing again almost immediately upon alighting. One male sang continuously and regularly while dodging my hand as I was trying to collect him. As with most meadow grasshoppers, disturbed males sometimes produce "incomplete" songs, omitting the last part. When two males are in close proximity, much more of the first part of the song is produced than ordinarily.

Song Records

*Franklin Co., O. (OSU Campus) 24 Aug. 1954, about 80° F., 226 songs in 2 min., 40 sec., 10 of these contained tick series.

*Franklin Co., O. (Clinton Twp.) 17 Sept. 1954, 85° F., 3 min., 60 songs per min., about 1/3 contain tick series. A male encounter occurs which involves a lot of tick series.

Hocking Co., O., 14 Sept. 1954, 18 songs in 15 sec.

Song Description and Analysis

The song of this species is a short phrase or buzz repeated rather regularly and continuously for long periods of time, at a rate of about one per second. The buzz, as shown in Plate XLIII, is less than a half second long, with a pulse rate of 75-80 per second. An occasional buzz has attached to its front as slower portion corresponding to the ticking part of the songs of Conocephalinae. This phase contains about 5 ticks at a rate of 35-40 per second, as shown in Plate XLIII. These are too fast to be counted, and merely give the phrase a non-uniform sound to the ear.

Although probably the loudest *Conocephalus* song treated here, this is still a soft sound, audible only a few yards away.

Descriptions given by Allard (1911c), Snodgrass (1928b), and Blatchley (1920, 6) for the song of this species, do not disagree with that given here.

Conocephalus strictus (Scudder)

The Straight-Lanced Meadow Grasshopper

Distribution

This species occurs from New York to North Carolina on the east coast, and west to Minnesota, South Dakota, Nebraska, Kansas, Texas, New Mexico, and Arizona (Rehn and Hebard, 1915, 6). Fox (1917, 6) found adults in Virginia August 31 to October 31, in open, undisturbed, dry grasslands, "especially partial to Andropogon, but taken also in Danthonia. Blatchley (1920, 6) says it matures about August 1 in Indiana, and is found in dry, upland meadows, open pastures, and prairies. Hubbell (1922a, 6) found adults from September 1 to 7 in dry, grassy fields and pastures, tall, dry grass and weeds along fences and roadsides, grassy borders of open woods, tall grasses and sedges in the drier margins of a ravine sedge marsh, and dry grass in a sandy field overrun with dewberry vines. Hebard (1938, 6) says adults appear in early August in Pennsylvania, in grasses on dry poor soil or sandy areas. Cantrall (1943, 6) found adults from July 27 to October 3 in the "mixed grass-herbaceous" habitat, as well as in clumps of panic grass in sparsely vegetated sand, and erratically in sunny oak-hickory near areas of "favorable habitat." Fulton (1932, 1951, 6) says this species occurs in grass, and sings from just past mid-July until November 1 at Raleigh, North Carolina.

In the present study this species has been encountered in Franklin and Hocking Counties, Ohio, and Wake County, North Carolina. At Columbus, Ohio, it has been heard only from September 1 to 20, and has undoubtedly been missed earlier and probably later in the season, due to its soft song. It is found in grassy spots, generally in company with brevipennis, but especially characteristic of dry, sparsely spots where brevipennis is rarely found.

Singing Behavior

This species sings day and night, and the singing males are usually very close to the ground, often in bluegrass within a few inches of the soil. Due to the softness of the song, the small size of the singers, and their habit of flattening lengthwise along plant stems, the singing males are very difficult to locate.

Song Records

*Franklin Co., O. (Plain Twp.) 17 Sept. 1954, 85° F., 1 min., 52 sec.

Song Description and Analysis

The song is a continuous, soft, fluttering buzz in which the speed of wing motion changes rather abruptly and noticeably, from about 10-16 pulses per second up to 40 per second. This change is apparent to the ear, and is the characteristic which most easily distinguishes the song of this species from those of the next two. Although no other authors have reported this characteristic, it was heard in North Carolina as well as in Ohio during this study. In the above recording, the singer started out with a rapid rate of wingstroke, slowed it at 4 seconds, then stopped at 11 seconds. At 14 seconds he started up again with the fast rate, slowed it at 15 seconds until 1 minute, then sang with the rapid rate again until 1 minute, 52 seconds, at which time recording ceased. The slow singing is not at a uniform rate, but varies from about 16 pulses per second to 10-12 per second. The transition from one speed to the other takes about ½ second.

This song has been described by Allard (1914, 6, Arlington, Virginia), Fulton (1932, 6, North Carolina), and Cantrall (1943, 6, George Reserve, Michigan). None of these authors mention the change in the speed of wingstroke described above.

Conocephalus nigripleurum (Bruner)

The Black-Sided Meadow Grasshopper

Distribution

This is a northern species with known southern limits at Alton, Illinois, Gibson County, Indiana (Hebard, 1934, 26), and Franklin County, Ohio. Rehn and Hebard (1915, 6) record it from New York, Ontario, Michigan, and Wisconsin. Blatchley (1920, 6) says it reaches maturity about July 1 in southern Indiana, and is found in tall rank grasses and sedges along shady margins of streams, ditches, large ponds, and lakes. Hubbell (1922a, 6) found adults September 2-7 in Michigan, in ravine sedge marshes and the rank herbaceous growth of lizard's tail marshes, and nymphs on July 10 among the Chamaedaphne and sedges around the margins of a nearly dry sphagnum bog on the inland side of sand dunes. Hebard (1938, 6) says this species appears adult in early July in Pennsylvania, and inhabits grasses and sedges in humid spots, with its northeastern limit at Ithaca, New York, and its southeastern limit at Milton, Pennsylvania. Cantrall (1943, 6) found adults from July 9 to September 21 on the George Reserve, Michigan, in the "wet shrub zone," and in semi-permanent and permanent marshes, usually in lower shrubs, but also on the main trunks and limbs of taller shrubbery such as dogwood, buttonbush, and high-bush huckleberry.

In the present study this species has been encounterd only twice, in a cattail marsh, with O. gladiator in Franklin County, Ohio (July 23, 1954), and in cattails along Lake Erie at Cedar Point (July 27, 1955) in company with O. volantum, O. delicatum, and C. attenuatus.

Singing Behavior

The only male heard singing in the field was captured during the daytime, a foot or so above the ground in rye planted alongside a marshy stream. He sang readily in the laboratory.

Song Records

*Franklin Co., O. (Mifflin Twp.) 28 July 1954, 81° F., 6 min.

Song Description and Analysis

The song is a continuous, soft, fluttering buzz, like that of C. attenuatus. The pulse rate is 18-20 per second at 81° F.

Cantrall (1943, 6) describes the song as a steady, even, rhythmic lisping.

Conocephalus attenuatus (Scudder)

The Lance-Tailed Meadow Grasshopper

Distribution

Rehn and Hebard (1915, 6) record this species from New York, Pennsylvania, west to Nebraska and Kansas, stating that it "apparently enjoys the most general distribution in the region south of the Great Lakes, and is probably very local and usually scarce everywhere east of the Appalachians." Its southern limits are Putnam, Illinois (Hebard, 1934, 26), Knox County, Indiana (Blatchley, 1920, 6), and Pickaway County, Ohio (present study). Blatchley (1920, 6) found it in company with O. volantum in tall, rank grasses growing in shallow water along marsh and pond borders in Knox County, Indiana. Hebard (1938, 6) says it reaches maturity in early August in Pennsylvania, and is abundant in tall vegetation near water. He says its eastern limits are Ithaca, New York, Sussex and Rancocas, New Jersey, and New Castle, Delaware. Hebard (1934, 26) records adults between August 9 and September 26 in Illinois.

In the present study this species was encountered only three times, between July 27 and September 28, in Licking, Erie, and Pickaway Counties, Ohio. In Pickaway County it was found in numbers in a large swamp with O. volantum. At Buckeye Lake in Licking County, it was found along the borders of a marshy pond, and in Erie County it occurred in cattails along Lake Erie, with O. *delicatum*, O. *volantum*, and C. *nigripleurum*.

Singing Behavior

This species apparently sings both day and night, and readily in captivity. The singing males are perched vertically on stems of tall weeds, cattails, etc., 4-7 feet above the ground, higher than any other *Conocephalus* species treated here.

This is a very wary species, extremely difficult to capture, and a disturbed individual will often jump repeatedly until completely out of sight. Blatchley (1920, 6) mentions the same type of behavior.

Song Records

*Pickaway Co., O. (west of Circleville) 28 Sept. 1954, 80° F., 5 min., 10 sec.

The song is a continuous, soft, fluttering buzz, with a pulse rate of 23-25 per second. It resembles the song of C. *nigripleurum* very closely, differing in the faster pulse rate.

Tettigoniidae, Decticinae

The Shield-Backed Grasshoppers

Introduction

The songs of 3 of the 10 eastern species in this subfamily have been recorded during the present study. Only one species occurring in Illinois, Indiana, and Ohio, was missed, Atlanticus americanus hesperus Hebard, a southern species with northern limits at Alto Pass, Illinois, and Fairfield County, Ohio (Hebard, 1934, 26). The 6 unrecorded species of Atlanticus are all eastern and southeastern. Idionotus sphagnorum (F. Walker) extends from northwestern Ontario to western Alberta and northward to Arctic America (Blatchley, 1920, 6).

Song descriptions for Atlanticus are largely absent from the literature. The only description found for eastern species not recorded here was that given by Fulton (1932, 6) for pachymerus. Walker (1911, 6) describes the song of I. sphagnorum.

All the species treated here overwinter as eggs and produce but one generation per season. A. testaceous (Scudder) hatches very early in the spring; first and second instar nymphs were active in great numbers in Franklin County, Ohio, on April 4, 1955. This is the earliest singing tettigoniid to mature in this area. Several adults were heard and collected near Hartford City in Blackford County, Indiana, on June 1, 1955, which is apparently an early record for this species.

The 3 species treated here were heard singing chiefly at night, though on one occasion a colony of testaceous was singing vigorously at noon on a bright sunny day.

All 3 species sing from weeds or brush, 2-5 feet above the ground, generally perched in a horizontal position. Their songs are rather soft, non-musical buzzes, either irregular or more or less regular in length and spacing, and often continuous for long periods of time. They can be heard only a few yards away except under very favorable conditions, such as on cold nights when the song is louder to human ears, and when there are no other insects singing in the area.

Atlanticus testaceous (Scudder)

The Short-Legged Shield-Bearer

Distribution

Rehn and Hebard (1915, 6) give the range of this species as from eastern Massachusetts west across Ontario, Michigan, and Minnesota, south to central Illinois and east across southern Indiana and central Kentucky to northern Virginia. They mention as doubtful the record of Scudder from Missouri. The earliest records for adults are June 6 (Blatchley, 1920, 6, Vigo County, Indiana) and the June 1, 1955, record for Blackford County, Indiana, given here. Rehn and Hebard cite October 15, Harrisburg, Pennsylvania, as the latest record.

Fox (1917, 6) found adults of this species from June 23 to July 16 in Virginia, on low shrubbery in dry, open woodland or wooded borders. Blatchley (1920, 6) found adults from June 6 until heavy frosts in Vigo County, Indiana, and says it occurs in dry, open wood-lands, thinly wooded rocky slopes, and borders of thickets. Hubbell

(1922a, 6) found adults from July 5 to 12 in oak dune forest, fields of second-growth scrub and margins of woods. Hebard (1934, 26) cites Illinois records of adults from June 10 to September 10. Hebard (1938, 6) says this species appears adult in early June in Pennsylvania, and is found in dead leaves and undergrowth of scattered deciduous forests, particularly of oak. Cantrall (1943, 6) found adults from June 20 to September 1 on the George Reserve, Michigan, in sunny and shady oak-hickory habitat, more abundantly in the former. He says that juveniles were taken in the mixed grass-herbaceous upland, but seldom more than 10-20 yards from woodland. He took no adults in such areas and says that erratic adults taken early in the season in the bog and semi-permanent marsh habitats were probably also derived from "wandering juveniles" and that they too must either "find a more suitable habitat or die."

In the present study this species has been encountered in Williams, Franklin, Hocking, Fairfield, Adams, and Coshocton Counties, Ohio, Blackford County, Indiana, and DuPage County, Illinois, between June 1 and September 14. Dense colonies were found along forest borders, in brushy pastures, fencerows, roadsides, and in open fields and bluegrass fencerows. A very dense colony, from which over 50 individuals were collected by random sweeping of the vegetation within a few minutes, was found dispersed across a ridgetop <u>Andropogon virginicus</u>-dominated, abandoned field situation in Hocking County, Ohio. At Blendon Woods in Franklin County, Ohio, nymphs were observed in great numbers as early as April 14. The young nymphs were, as mentioned by

Cantrall, dispersed from the border of a dry hickory forest out into a brushy and eventually open bluegrass pasture. Later in the season the singing males are heard chiefly along the forest border. The tremendous numbers of young nymphs as compared with the relatively small number of adults later in the season indicates a high rate of mortality in the juvenile stages.

Singing Behavior

This species is chiefly a night singer, but the colony noticed in Blackford County, Indiana, on June 1, 1955, was singing vigorously although it was a warm clear day near noon, and these individuals were in a mowed bluegrass fencerow, completely in the open and exposed to the full light and heat of the sun. During several daytime visits to Blendon Woods in Franklin County, Ohio, the considerable numbers of males along the road through the woods were never heard, though they sang noisily during dusk and evening visits to the area.

Singing males are usually perched 3-5 feet above the ground in a horizontal position on leaves or horizontal branches of the tallest weeds or bushes in the area. This is similar to the habits of Scudderia and Amblycorypha, and in contrast to the Conocephalinae and Neoconocephalinae which usually perch more or less vertically, and not generally on the tops of the vegetation, but rather down inside it, though near the top. All the males of this species seen during the day were on or near the ground.

Males of the short-legged shield-bearer are stimulated to song by the beginning of singing by their neighbors, and this leads to a gradual increase in the number of males singing in a colony until practically all seem to be singing together. Gradually the individuals drop out one by one until the colony is completely silent again after a few minutes of song. Within a minute or so the cycle begins again and is repeated over and over, much as in *Amblycorypha rotundifolia*, or less apparently, *A. oblongifolia* and *A. uhleri*. This behavior is well described by Cantrall (1943, 6) for the colonies he observed in Michigan. Caged males are definitely influenced by each other's singing, and when 4 or 5 are caged together, the same reaction is observed as described here for colonies in the field. This has been noticed and recorded on several occasions.

Singing males space themselves in the field and are sedentray, remaining on the same plant throughout their daily song period, and probably in a relatively small area throughout their entire adult lives.

Song Records

*Blackford Co., Ind. (near Hartford City) 1 June 1955, 3 min., 85° F. (lab)

*Franklin Co., O. (Blendon Woods) 18 May 1954 (reared in lab), 80-85° F., 8 min.

*Adams Co., O. (Lynx) 9 July 1954 (1) 65° F., 40 sec. (2) 85° F., 50 sec. (lab)

Franklin Co., O. (Blendon Woods) 6 July 1955 (1) 70.5° F., 15 sec. (2) 35 sec. (3) 70 sec. (4) 5 specimens caged together, 83° F., 1 min., 15 sec.

Song Description and Analysis

This song is a series of soft buzzes of irregular length and spacing, which are repeated for a few minutes at intervals of a minute or more. The buzzes last anywhere from ½ second up to several minutes, and are usually separated within songs or series by intervals of only a fraction of a second. The pulse rate, as shown in Plate XII, varies from 7.6 per second at 65° F. to 25 per second at 90° F. A great deal of individual variation exists in this respect, and on one occasion, a recording made of two individuals singing together in the same cage revealed that one was singing with a pulse rate of 24 per second, the other at only 16 per second. The Vibragrams (Plate LII) show an alternation of like pulses, or pairing of pulses, indicating that each wingstroke probably produces two sound pulses, or in other words, the wingstroke is acoustically effective in both directions. Thus the rate of wingstroke above would have been only 12 and 8, respectively. This "double-pulse" type of singing seems to occur in all the Atlanticus species recorded in this study.

Often when several individuals caged together are singing, the effect of continuous singing is produced, with different individuals filling in the gaps between buzzes.

This song has been described by Davis (1893, 6, Staten Island, New York), Allard (1911e, 6, Plummer's Island, Maryland), Cantrall (1943, 6, George Reserve, Michigan), and Pierce (1948, 26, Franklin, New Hampshire). These descriptions agree essentially with the above. Pierce obtained 13-21 double pulses per second and a frequency of 14.96 kps.

PLATE LII. CALLING SONGS OF DECTICINAE

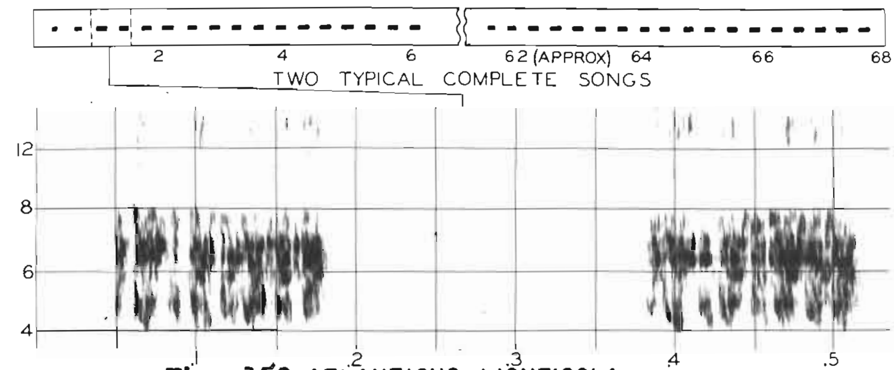


Fig. 159. ATLANTICUS MONTICOLA

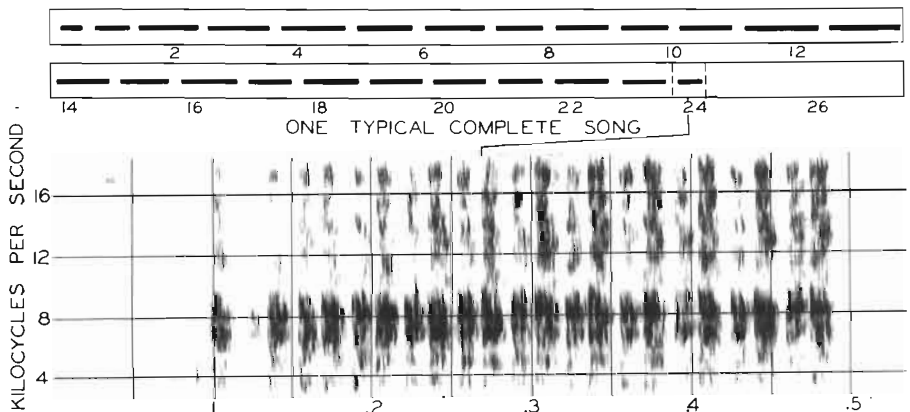


Fig. 160. ATLANTICUS DAVISI

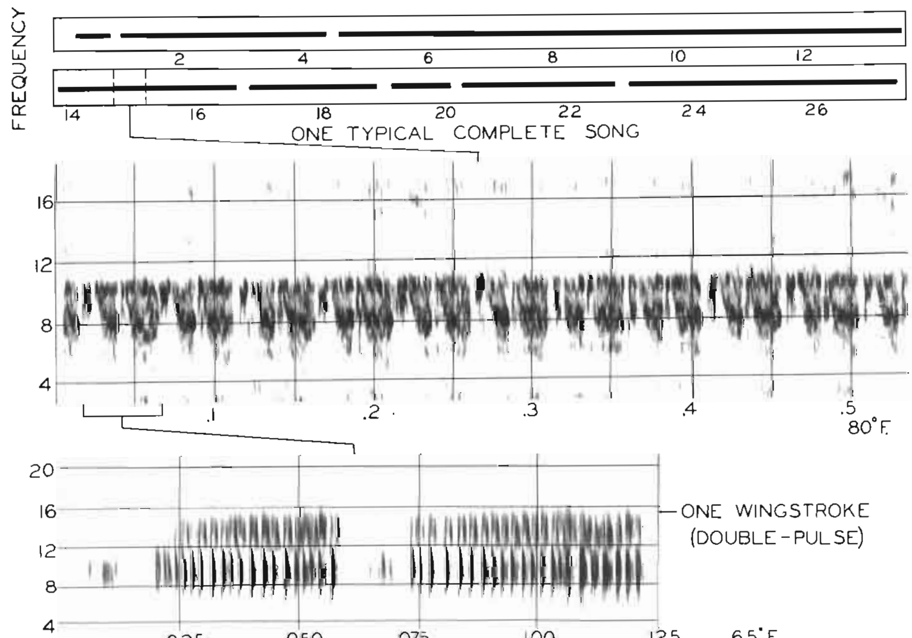


Fig. 161. ATLANTICUS TESTACEOUS

TIME IN SECONDS

<u>Atlanticus davisi</u> Rehn and Hebard

Davis' Shield-Bearer

<u>Distribution</u>

Rehn and Hebard (1915, 6) say this species ranges from northern New York south to south-central Virginia, west to southern Iowa. They say it occurs adult between the latter half of June and early July, and the first week of September, and they took it in a "variety of situations," in company with <u>testaceous</u> at Arlington, Virginia, and with <u>americanus</u> at Orange, Virginia. In the latter locality they say it is "locally not scarce in dead leaves and scattered green undergrowth of chestnut woods on Southwest Mountain. Fox (1917, 6) found adults from August 20 to September 6 in Virginia, in grassy and shrubby undergrowth of dry mountain woods. Blatchley (1920, 6) found adults from June 4 to September 28 in southern Indiana, on high, rocky, thinly wooded slopes. Hebard (1938, 6) says this species appears adult in early June in habitats similar to those of <u>testaceous</u>.

In the present study this species was encountered but once, in a damp forest in Franklin County, Ohio, on July 27, 1954. Several males were heard singing at night in the forest undergrowth.

<u>Singing Behavior</u>

Caged males sang readily both day and night, but more continuously after dark in the laboratory. In the field the singing males were perched horizontally on leaves of weeds and bushes 3-4 feet above the ground.

Song Record

*Franklin Co., O. (Blendon Twp.) 27 July 1954, 85° F., 3 min., 30 sec.

Song Description and Analysis

The song is a series of short, soft buzzes, delivered at a rate of about 1 per second (Plate LII). These buzzes may be produced continuously for several minutes, but more often are delivered in groups of 15-30, separated by longer intervals of from several seconds to a minute or more. The pulse rate within the buzzes is about 60 per second, indicating a wingstroke rate of 30 per second, since the wingstrokes appear to be acoustically effective in both directions. In one series of 77 buzzes, requiring 1 min., 12 sec., the number of pulses per buzz ranged from 18 to 28, but was most often 20-24.

Atlanticus monticola Davis

The Mountain Shield-Bearer

Distribution

Rehn and Hebard (1916, 6) say this species occurs in the more elevated areas of the southern Appalachians from Durbin, West Virginia, to Clayton, Georgia. They found it in the undergrowth of the deciduous forest immediately below the spruce belt at Jones' Knob, North Carolina, and give the dates for adults as from July 28 (Linville, N. C.) to

October (Jones' Knob).

In the present study a single male of this species was collected in Pocohontas County, West Virginia, on August 11, 1955, near a female on a bush along the edge of the woods in the mountains. They were parched about 2 feet above the ground, and the male was singing (night). The female escaped, and the male was later identified on the basis of his song by comparing it with the description given by Fulton (1932, 6), and with the help of Dr. E. S. Thomas.

Song Record

*Pocohontas Co., W. Va., 11 Aug. 1955, 85° F. (lab), 5 songs at intervals of about a minute, each song (buzz series) lasting 5-8 sec.

Song Description and Analysis

This song is a series of soft buzzes, like those of the preceding two species. The buzzes here, however, contain 1-5 wingstrokes (2-10 pulses), and there are 19-21 buzzes per series, or song. The wing-stroke rate is about 30 per second, and the buzz interval about 0.2 second (Plate LII).

Fulton (1932, 6) described the song of this species from North Carolina (observed at 55° F.), as " a soft, rasping sound, each note plainly of 3 wing movements. Notes repeated about two per second when regular, but there are many longer pauses so that the actual rate varies from 10 to 16 in 10 seconds."

Tettigoniidae, Tettigoniinae

Hubbellia marginifera (F. Walker)

Distribution

This species, the only representative of this subfamily in North America, was described by Hebard as praestans in 1927, from a single female collected by T. H. Hubbell in Liberty County, Florida, along the Apalachicola River. This female was perched on a tall weed directly beneath a tall pine, and near a clump of Torreya on the lip of a ravine. Hebard placed this species in the Decticinae.

Uvarov (1940, 26) pointed out that this was apparently the same insect described in 1869 by F. Walker as Locusta marginifera, and Uvarov placed it in the Tettigoniinae. Though the locality label on Walker's specimen was "Africa," Uvarov believed this to be erroneous, since the collection containing this insect had a specimen of Chortophaga viridifasciata (DeGeer) with no label alongside specimens labelled "Africa" and South Africa". Hubbell added a note to Uvarov's paper to the effect that he thought it probable that this species was "thamnophilous or even arboreal." He believed that it inhabited the ravine forest rather than the dry, oak- and pine-covered sandy uplands of the type locality.

This species was heard singing in abundance around Raleigh, North Carolina, August 8-10, 1955, at night in tall pines. All the males heard were at least 20 feet above the ground, and the 3 seen were perched on the upper surface of horizontal branches. One male and one female were collected by climbing the tree after locating the specimens with flashlights. In pine forests north of Raleigh the song of this species was very common throughout the night, but 3 of us, armed with flashlights, were able to collect only 2 specimens over a period of about 2 hours.

Song Record

*Wake Co., N. C. (McCuller's Pond) 8 Aug. 1955, 76° F., 32 chirps in 45 sec.

Song Description and Analysis

The song is a continuous and regular repeating of a chirp or phrase containing 3 pulses (Plate XLIII). Each successive pulse in the chirp is longer than the preceding. It is a non-musical and rather high-pitched sound, resembling in quality the lisp of *Microcentrum rhombifolium*. It is not particularly soft, and can be heard perhaps 50-100 yards away. The above recording is a poor one, and the Vibragram was made by trimming out the noise at the bottom of the graph which did not reach quite to the most intense frequencies of the insect sound, due to its high pitch.

The Evolution of Sound Production and Mating Behavior in the Orthoptera

The Orthoptera constitute one of the best-known orders of insects, for a number of reasons. The order is a small one, and its members are, in general, large, easily captured, easily reared insects. It is one of the oldest and most primitive orders of insects, and has left a fossil record less scanty than those of most other orders. Perhaps most important of all from the point of view of phylogenetic relationships. the Orthoptera enjoy the unique distinction of having living with them today, a close approximation of their ancestors of 250 million years ago. The Blattidae, or cockroaches, are the only living family of insects known to have existed as long ago as the Carboniferous, and the common orthopteroid ancestor was a blattoid insect, very much like present-day roaches. Carpenter (1953, 26) says, "The differences between the ancient roaches, existing some 250 million years ago, and those of today, is exceedingly slight, involving chiefly position of wing veins."

All of the major groups of modern Orthoptera contain species that produce special sounds of one sort or another. However, only a relatively few species are involved in the Phasmidae, Mantidae, and Blattidae, and in each of these families the structures and behavior patterns associated with sound production seem to be of comparatively recent origin, and unique to the family. On the other hand, sound communication is well-developed in the remaining Orthoptera and practically universal in several groups. Some of the behavior patterns and structures associated with the system of sound communication occurring in the Tettigoniidae, Gryllidae, and Gryllacrididae are of ancient origin, their rudiments appearing in the Paleozoic ancestor of all modern Orthoptera. In this group, sound communication arose in connection with mating, and largely because of the cockroaches and our extensive knowledge of the phylogenetic relationships of the Orthoptera in general, it can be traced from its beginnings two or three hundred million years ago. If for no other reason this is interesting from the fact that it is the first record of specialized sound production in any group of organisms.

The first indication that the behavior of modern roaches can tell us something about how sound production developed in the Tettigoniidae and Gryllidae is connected with their rather unique courtship procedures and copulatory position. According to Roth and Willis (1954), in most of the winged roaches the male lifts his forewings or tegmina, exposing dorsal glands on the abdomen which are attractive to the female. The female begins to feed on the secretions in these areas, and eventually mounts the male under his lifted forewings, and copulation occurs in this position. In many species, according to these investigators, the male rotates out from under the female after the genitalia are engaged, and copulation is completed in an end-to-end position. This courtship and mating procedure has been similarly described to me by William Butts, Jay A. Buxton, and William Hahnert of the Department of Zoology and Entomology of the Ohio State University, for <u>Periplaneta</u>

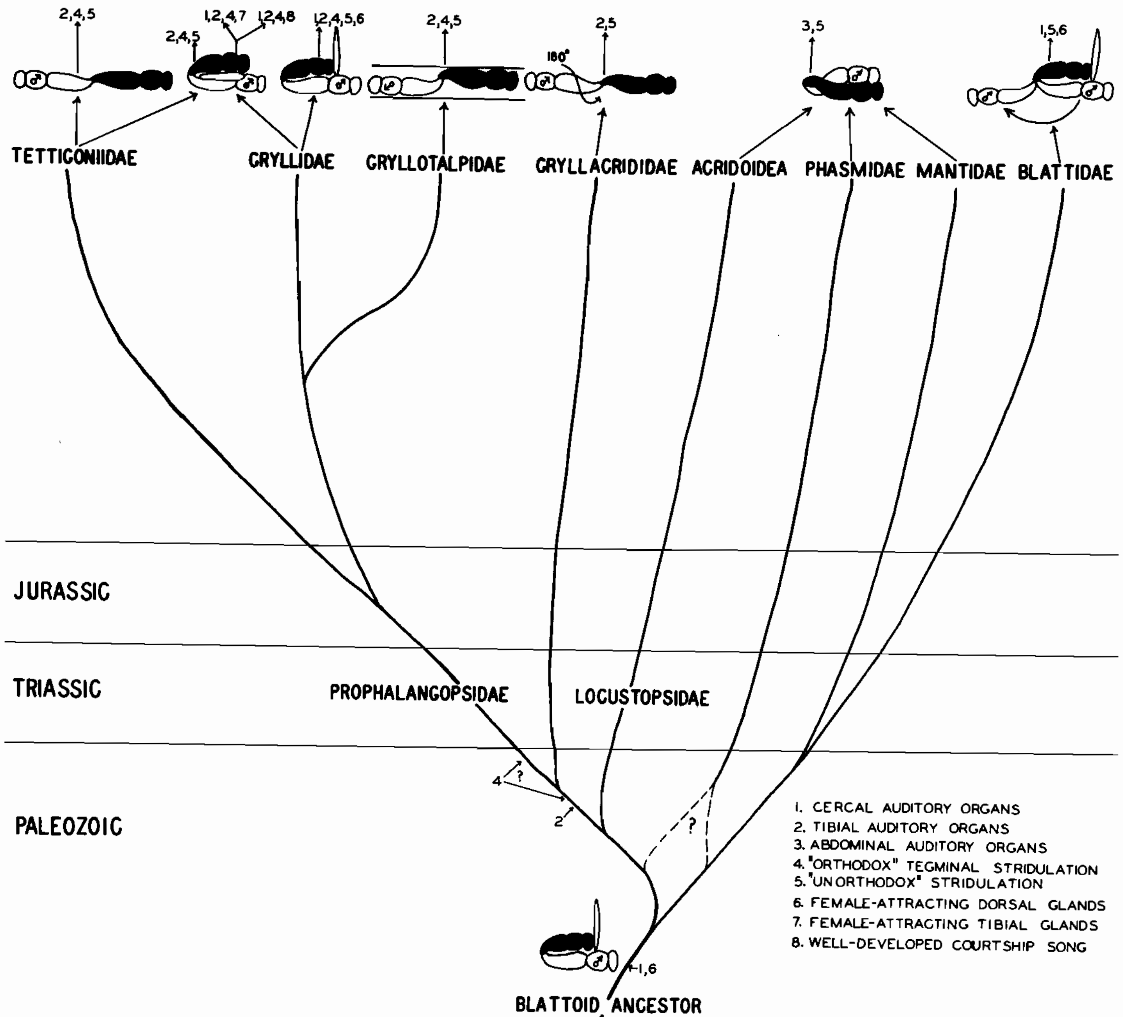
americana (L.), Blattella germanica (L.), and Supella supellectilium (Serville). Later I was able to observe it myself in the first two of these species.

This seems to be a rather specialized and unusual courtship and mating procedure, yet it is duplicated almost exactly in three subfamilies of the Gryllidae, the Oecanthinae, the Eneopterinae, and the Trigonidiinae, and in at least two genera of the subfamily Phaneropterinae in the family Tettigoniidae (Fulton, 1930, 6, and Isely, 1941, 6). In the Gryllidae, however, the lifting of the forewings is also associated with the production of sounds by means of specialized structures which occur on them, and the attractive glands consist of a highly differentiated metanotal gland, rather than the widely distributed and vaguely differentiated glandular areas occurring on the abdomens of male roaches. In the Phaneropterinae which lift their tegmina before the female, there apparently is no sound production associated with this act, and the dorsal glands, if such exist, are so poorly differentiated that they have not as yet been observed.

This copulatory position is diagramed on the phylogenetic tree in Plate LIII. The female often spends some time feeding at the secretion of the metanotal gland before actual transference of the spermatophore takes place. The male tree cricket sometimes vibrates his wings briefly while this courtship is going on, producing short, irregular bursts of sound with the specialized structures located on them. Anaxipha exigua (Say) produces a quite distinctive song in this

PLATE LIII. Fig. 162

EVOLUTION OF SOUND PRODUCTION AND MATING BEHAVIOR IN ORTHOPTEROID INSECTS



situation (Plate XLII). The cockroach also sometimes vibrates his wings, but he possesses no specialized structures such as those found in the crickets, and the result is only a faint rustle.

The complexity of this courtship procedure, and the great similarity between these two groups, makes it almost certain that their common ancestor behaved in a manner practically identical to that of the modern roaches. Yet, as shown in Plate LIII, these two groups supposedly diverged in the Paleozoic, before any of the other major groups of modern Orthoptera had separated, indicating that all the modern groups of Orthoptera descended from an insect which behaved in this same manner. This seems questionable when it is noted that three groups of modern Orthoptera, the Acridoidea, the Phasmidae, and the Mantidae, all of which may have arisen independently, copulate with the male mounting the female. However, as reported by a number of authors, such as Green (1898, 26), Cantrall (1943, 6), Rau and Rau (1913, 26), Stockard (1908, 26), Federov (1927, 26), and Srivastava (1956, 26), and personally observed in a number of Acrididae, in all three of these groups the male curls his abdomen down under that of the female, either from the right or the left side, indicating that each of them did, in fact, develop from an ancestor in which the position was reversed, with the female on top, as it occurs in the cockroaches.

Plate LIII traces the evolution of the structures and behavior patterns connected with sound production in the modern Tettigoniidae and Gryllidae from their beginnings in the courtship procedure of the

Paleozoic orthopteroid ancestor. The phylogenetic arrangement used here is a composite of those proposed by Turner (1916, 26), Crampton (1919, 26), and Walker (1922, 26). This arrangement has been confirmed to my own satisfaction, using data from various studies, such as those of Nesbitt (1941, 26), Schmitt (1954, 26), and personal observations. The point of origin of the Phasmidae remains uncertain, but that is not of importance in the present discussion. In addition, certain groups of Orthoptera have been left out since there is no information at hand concerning them which would alter this discussion in any way.

The evidence so far indicates that the common ancestor of the Orthoptera possessed generalized female-attractive dorsal glands and mated with the female mounting the male (or the male backing under the female) under his raised forewings, which he perhaps vibrated a little. Thus there was involved at least chemical, and probably also visual stimulation for the female.

Sometime later, either before or after the Acridoidea branched off, tibial auditory organs began their development, and the jiggling of the tegmina became associated with the production of sound, adding a new, auditory stimulus to the mating system. The first behaviorally significant sound produced by the ancestor of the Tettigoniidae and Gryllidae was probably in a sort of courtship sequence. From there on it is easy to visualize the rapid increase in importance of the auditory stimulus, the modification and increased efficiency of both the organs producing sound and those perceiving it, and eventually the presence of an auditory stimulus sufficient to attract the female from outside the range of her other senses, which is apparently the case with the "calling song" already described as being produced by the males of these two groups.

Now we have skipped rather quickly over the tibial auditory organs and how they might have arisen. These organs, according to Pumphrey (1940, 6), consist of a thinned region in the exoskeleton, the primary tympanic membrane, associated with air sacs and a chordotonal organ. Chordotonal organs, or structures similar to those found associated with tympanal organs, are found on many different parts of the bodies of insects, as are tympanal organs, in the different orders. Rather prominent chordotonal sensilla are found in the tibiae of the second and third legs of tettigoniids and gryllids in a position corresponding to that of the tympanal organs of the foretibiae, according to Pumphrey, who states, "It seems relatively certain, although there is no direct evidence, that the primary function of chordotonal sensilla is a proprioceptive one — to register the displacement of one part of the skeleton with respect to another..." Thus, this organ may have required only slight alteration to become functional as a crude auditory organ, and with the male producing slight rustling noises incidental to wing vibration involving visual stimulation for the female during courtship, we are presented with one possible method for the origin of sound perception along with sound production. In this hypothesis it is logical that the chordotonal organs on the forelegs should develop into auditory organs rather than those on the other two pairs of legs, since in the courtship procedure involved, the male backs toward the head of the female.

Pumphrey and Rawdon-Smith (1936, 26) point out that the long, hair sensilla on the cerci of cockroaches, crickets, and locusts can also act as auditory organs, and the question may arise as to whether these organs had any significance in the origin of infraspecific sound communication in the Gryllidae and Tettigoniidae. Rau (1940, 26) investigated the behavior of roaches in response to several different kinds of sounds, and was able to observe only an escape response to loud sounds. It seems doubtful that the cercal auditory organ ever had any place in infraspecific sound communication in these insects.

The Acridoidea present a sort of puzzle. They apparently left the tettigoniid-gryllid stem before the development of tegminal sound production and tibial auditory organs, and they have diverged considerably from these groups in many respects. Yet they later came along with their own system of sound communication, based on completely different structures, but in general functionally analogous to the system occurring in the Tettigoniidae and Gryllidae. Stridulatory structures have arisen a large number of times in the Acridoidea, and in many different places on the body (see Kevan, 1954, in Busnel, 1954, 6, p. 103), but the "orthodox" method involves the tegmina and the hind femora. The tympanal auditory organs of the Acridoidea are located on the first segment of the abdomen.

The sound-producing Gryllacrididae also bring up a question, since some of them at least have tibial auditory organs like the Gryllidae and Tettigoniidae, but femoro-abdominal sound-producing organs (Ander, 1938, 6). Either they once had tegminal sound organs but lost them, retaining the tibial auditory organs, or the tibial auditory organ developed before the tegminal sound organ (see discussion, p. 140-141, Fusnel, 1954, 6).

In some of the present-day Eneopterinae and Trigonidiinae, which appear to be losing their tegminal sound organs, the tibial auditory organs have degenerated along with the degeneration of the sound organs. The bush cricket, Hapithus agitator Uhler (Eneopterinae), has been observed in stridulation only once (Fulton, 1932, 6). The sound Fulton heard was a soft, creaky noise made by a male following a female around in a cage. He later examined the stridulatory vein of a male of this species and found that it had only 35 rather widely spaced teeth. In two Ohio specimens examined, no tympanal organ at all could be found on the foretibiae of the male, and on the female they were represented by small, oval, poorly differentiated areas on both the inner and the outer faces of the tibiae, distinguishable chiefly by the fact that they were hairless while the rest of the tibia was sparsely clothed with short hairs. Apparently it is not known whether the male of this species possesses a metanotal gland, but nearly all the old males collected in the field have the middle base of the tegmina eaten away, sometimes nearly up to the metanotum. It is possible that chemical stimulation for the female still exists, but the male does not lift his tegmina in her presence, or, less likely, some "searching" behavior by the female may still persist in the absence of chemical stimulation.

The cricket Falcicula hebardi Rehn (Trigonidiinae) still possesses vestigial sound-producing structures. Fulton (1932, 6) found 30 faint cross ridges on the stridulatory vein and was unable to find any trace of tibial auditory organs. It has never been heard to sing.

Uvarov (1954, 6, in Busnel, 1954, 6, p. 141) points out that in the subfamily Catantopinae of the Acrididae, almost all of the species possess tympanal organs, but very few have stridulatory organs. Uvarov and Kevan both emphasized in this discussion that in the Acrididae the presence and degree of development of the tympanal organ seems more closely related to the presence and degree of development of the tegmina than to the presence of sound-producing mechanisms, as one might expect.

As illustrated in Plate LIII, the rather complicated set of structures and behavior patterns that apparently characterised the courtship procedure of the Paleozoic orthopteroid ancestor has followed quite different paths in the different groups that have developed at later times. In the Tettigoniidae and Gryllidae these characters have developed into a highly successful and complex system of sound communication. In the Blattidae the same structures and behavior patterns have remained relatively unchanged for two or three hundred million years. In the Acridoidea they were lost, then the same group later developed sound communication based on entirely different structures and behavior patterns, but in many respects highly analogous in function. In the Phasmidae and Mantidae these characteristics were lost and nothing comparable to them has developed since.

By comparing the structures and behavior patterns associated with sound production in the modern Tettigoniidae and Gryllidae, and the "structure" of the sounds themselves, we can reconstruct some of the evolution that has occurred since the separation of these two families sometime in the Jurassic (Zeuner, 1934, 6).

In both the Gryllidae and Tettigoniidae, the usual pattern is that the males are sedentary, spacing themselves somewhat, sometimes in colonies, and producing a calling song which attracts the female. Their common ancestor probably behaved very similarly, and must also have possessed a courtship song which he produced when approached by a female. Apparently none of the modern Tettigoniidae produce what could be called a courtship song, but the majority of the crickets produce some sort of sound around the female prior to copulation. In the Oecanthinae the calling song and the courtship song are very similar, and this was probably the case in the Jurassic ancestor of the Tettigoniidae and Gryllidae.

This Jurassic ancestor must also have possessed dorsal, female-attracting glands, since these occur in both Gryllidae (Fulton, 1915, 6) and Tettigoniidae (Fulton, 1930, 6, and Isely, 1941, 6). He may have possessed some sort of sound response similar to the fight sound. It is unlikely that any sort of protest sound was produced by this insect, since such a response is known in only a few species of Tettigoniidae (*Pterophylla camellifolia camellifolia*, see p. 274; *Amblycorypha oblongifolia*, see Blatchley, 1920, 6). In *Pterophylla* the protest sound, produced by a captured or disturbed individual, is quite similar to the sound produced by two males when they happen to get very close together in the field. In this case the protest sound may represent an extension of the fight sound stimulus situation, and probably was the last kind of sound response to develop in these insects. This is rather interesting, since it seems probable that in all or most other insects, including the Cicadidae, the protest note may have been the first, or one of the first responses to evolve, possibly in connection with struggling movements made by captured individuals.

The sound-producing structures of male Tettigoniidae and Gryllidae are located on the tegmina or forewings, and consist of a transverse row of tiny teeth called the file, located on a heavy vein on the ventral side of the upper tegmen near its base, and a dorsally-projecting, sharp-edged scraper on the median edge of the lower tegmen. In crickets, the files and scrapers on the two tegmina are equally well-developed. Generally the right tegmen is uppermost, making the scraper on the left tegmen and the file on the right tegmen the functional pair. However, a few crickets can be found with the left tegmen uppermost and in the one specimen I have observed (mountain Acheta), the song was no different from that produced by right-winged crickets. If the positions of the tegmina are reversed in a non-teneral specimen, he will, after a moment, jerk his wings a few times, then flip them back to the original position. Lutz, 1906, 6, reversed the tegmina in a teneral male and states that this male remained left-winged, and later sang as well as any other.

In the Tettigoniidae the left tegmen is uppermost, and the functional file and scraper are much more highly developed than the non-functional ones.

The venation of the tegmina in male Gryllidae is greatly modified, with variously-shaped, membranous, drum-like areas occurring over most of their surfaces. The veins which remain are heavy and stiffened, possibly causing the wing to vibrate during sound production more or less as a single unit. In the Tettigoniidae, on the other hand, only the veins near the base of the tegmina show any great modification, and the two tegmina are not always identical in the degree and kind of modification. Often only a single drum is present on the right tegmen and none on the left (see Plates II, III).

Plate IV contains diagrammatic drawings of the file and scraper occurring on the tegmina of the house cricket, <u>Acheta domestica</u> L., and Plate V shows drawings of the file and scraper of the oblong-winged katydid, <u>Amblycorypha oblongifolia</u>. As shown by these drawings, the file teeth on the tegmina of Gryllidae are much smaller and more closely spaced than those occurring on the tegmina of Tettigoniidae, and often present a much more complicated appearance. In all specimens examined of both families, the file teeth point toward the median edge of the tegmen. In apparently all of the Gryllidae and most of the Tettigoniidae the file and scraper are in contact only during the closing of the tegmina, thus the scraper moves "against" the slope of the teeth. In some Tettigoniidae (<u>Atlanticus</u> and some

Orchelimum), the file and scraper are apparently in contact both during the opening and the closing of the tegmina, producing a double-pulse of sound with each wingstroke, or an alternation of like pulses rather than a succession of like pulses. As shown in Plates IV and V the scraper is probably a highly flexible structure, being mounted along the edge of a rather thin, membranous area.

The above-described differences between the structure of the tegmina of Tettigoniidae and Gryllidae are undoubtedly associated with certain fundamental differences in the structure of the sounds produced by members of these two families. The sounds of Gryllidae are usually completely dominated by a pure frequency, except in the courtship songs of the Gryllinae. This has been clearly demonstrated by Busnel (1953, 6), and is revealed in the graphs of cricket songs in this paper. A Vibragram of a cricket song takes the same shape as one produced by graphing an audio-oscillator note. However, if the intensity of the signal is increased, a practically continuous spectrum appears on the Vibragram, showing that there are very soft "impurities" in the sound, which are obscured by the dominant pure frequency.

By contrast, the sounds of Tettigoniidae are noise-like, or contain a wide frequency spectrum, and are never greatly dominated by a pure frequency.

The exact mechanism responsible for the dominant frequency in cricket songs is still a subject of some disagreement between different investigators. Lutz and Hicks (1930, 6) believed that any resonant vibrations of the wing would be quickly damped by air resistance, and suggested that this pure frequency might be due to the up-and-down waves of the entire wing each time the scraper moves across a tooth of the file. Pasquinelly and Busnel (in Busnel, 1954, 6, p. 148) agree with this, but add the possibility that rather than the rate of toothstrike being responsible for the frequency, the resonant vibration of part or all the wing may be, in a sense, responsible for the rate of toothstrike. They point out that if the scraper were merely held against the file teeth with a certain pressure, not sufficient to cause it to jump from tooth to tooth, and the wing vibrated with a certain resonant frequency (apparently after the first toothstrike), this vibration might be sufficient to cause the scraper to jump from one tooth to the next at a rate corresponding to the resonant frequency. In such case, we would have to say that the toothstrike rate depended on the resonant frequency rather than vice versa, or the two are interrelated in such a way that we would not expect much of a change in toothstrike rate or much of a change in frequency within the song of a single insect.

Pierce (1948, 26) says merely that the dominant frequency is a "file-teeth impact frequency" (p. 102).

While no concentrated effort has been made in this study to determine what exact mechanism is involved in this situation, certain indications have appeared which are worthy of mention.

First of all, as demonstrated in Plate XIV, with a drop in temperature, and presumably in actual speed of wing motion (distance covered per unit time), there is a corresponding drop in the dominant frequency in cricket songs. Second, as shown in many of the Vibragrams of cricket sounds, there is a noticeable drop in frequency within each sound pulse (sound caused by one wingstroke), producing a downslurred note. This could either be due to a slowing of the speed of wing motion during the file-scraper contact, or to a differential spacing of the teeth of the file, or to a combination of these two factors. Examination of the file in various species of Oecanthus and Acheta indicates that the file teeth are somewhat more widely spaced in the center of the file than at either end.

In summary, if the dominant frequency in cricket songs were due to or controlled by a resonant frequency of the whole or some part of the wing, we would not expect to find the changes in frequency pointed out above. On the other hand, if the dominant frequency is caused by the rate of toothstrike which in turn is determined by the speed of wing motion and the spacing of the file teeth, we would expect exactly the variations shown above. If a resonant frequency is important, the only alternative would be that this frequency changes with temperature, and that it also changes during the acoustically effective portion of the wingstroke. This would not seem to be the simplest hypothesis. It should be noted, however, that Busnel could find no change in frequency in the song of Oecanthus pellucens Scop., such as has been shown for the species treated in this study.

As revealed in the Vibragrams, there are several vibrations after each toothstrike in the songs of Tettigoniidae, and a wide frequency spectrum is involved. Pierce (1948, 26) gave very exact frequencies for many of these species, and his figures probably correspond to one of the dominant frequencies in the sound. Pielemeier (1946, 6), using a sound level meter, has given frequency spectra for several American species, and Busnel (1953, 6) gives frequency spectra for several European Tettigoniidae. The work of these investigators shows that in the sounds of many species of Tettigoniidae there are frequencies extending up to 50, 60, and even 100 kilocycles per second. The equipment used in this study does not permit the analysis of such sounds, and no claim is made for the accuracy of any part of the frequency spectrum shown in the Vibragrams above 15 kilocycles per second.

The positions of the tegmina during the calling songs, and the courtship songs or displays of the Tettigoniidae, Gryllidae, and Blattidae are shown in Plate LIV. In the tree crickets, bush crickets, and sword-bearing crickets, the primitive position of approximately a 90° angle with the body is assumed in both the calling song and the courtship song and display. The chief differences in the behavior of a male singing the calling song and one courting a female in these groups is that during the courtship the rhythm of the song is altered slightly, and he often vibrates his wings noiselessly at times while backing toward the female, and after she has mounted and begun to feed at the secretions of the dorsal glands. The courtship songs of these crickets are poorly differentiated from their calling songs.

Lifting of the tegmina during courtship display also occurs in the Blattidae and in certain Phaneropterinae. Neither of these produce

PLATE LIV. TEGMINAL POSITION IN ORTHOPTERA

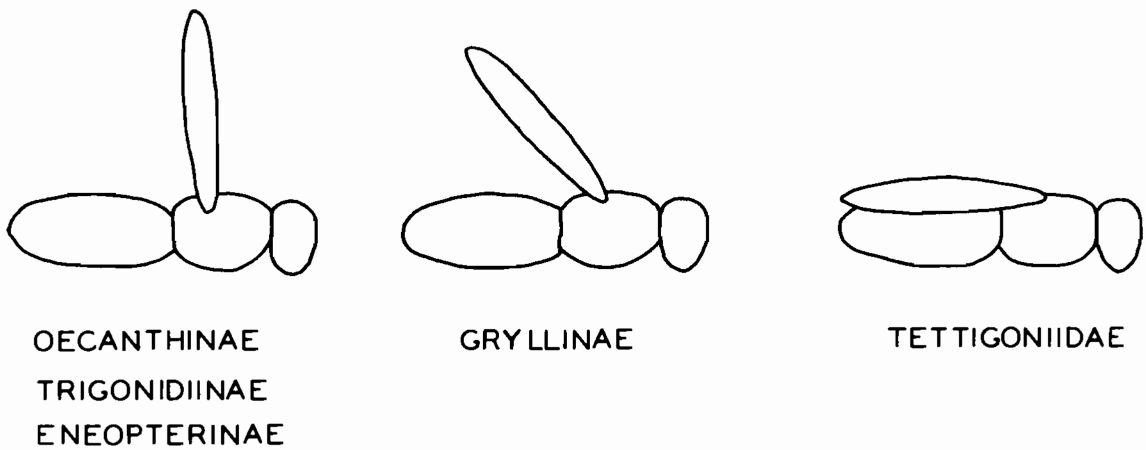


Fig. 163. SOLITARY OR CALLING SONG

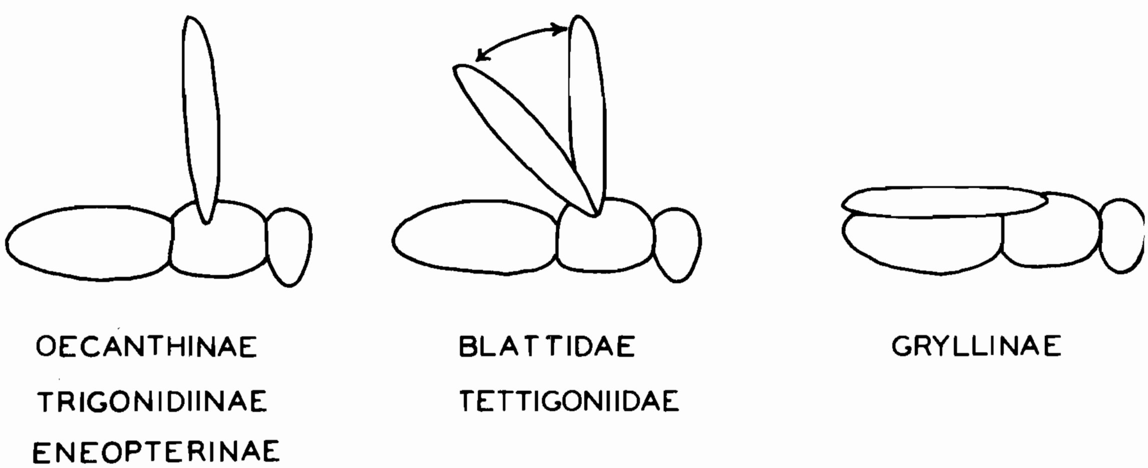


Fig. 164. COURTSHIP SONG OR DISPLAY

any significant sounds while in this position, although the Blattidae vibrate their wings, producing a slight rustle.

The Gryllinae have lost the dorsal glands, and somewhat different positions are assumed during sound production and copulation. In the calling song the tegmina are lifted to about a 45° angle, and in the courtship song they are scarcely lifted at all, but are merely tilted roof-like over the abdomen and more or less rotated, so that only the dorsal fields are opened and closed. The female mounts on top of the flattened tegmina. The position of the tegmina during the calling song and the fight chirping is shown in Figure 3 (Plate I).

The Gryllinae have developed courtship sounds which are usually quite distinct from the calling songs (Plate XXXIV). In both the Gryllinae and the crickets which lift their tegmina to a 90° angle and possess a metanotal gland, a visual stimulus for the female may still be involved in courtship. This is suggested by the noiseless vibration of the tegmina during courtship in the Oecanthinae, and by the "exaggeration" of the motion of the tegmina in the courtship songs of the Gryllinae. The motion of the tegmina in the courtship songs of these species is much more obvious and more easily followed with the eye than in the calling song. However, Khalifa (1950, 6) found that the house cricket courts and copulates normally in the dark, and his experiments indicated that the amount of time required for courtship was no longer in the dark than in daylight.

An interesting variation in courtship procedure occurs in several species of <u>Nemobius</u> (Fulton, 1931, 6). Here a female-attracting gland has developed in connection with one of the spines at the base of the hind tibiae, and the courtship songs have largely been lost. During courtship and copulation the male holds his hind legs up over his back, the female mounts on top of the flattened tegmina and feeds on the secretions of the tibial gland. Why these insects should lose their dorsal glands in favor of a courtship song, then apparently lose the courtship song in favor of glands again is a good question. Presumably this has been the case. A "chirp" apparently associated with courtship in Nemobius carolinus and N. palustris has been observed in caged specimens during this study. Apparently these have not been noted by previous workers.

As shown in Plate LIV, male Tettigoniidae scarcely lift their tegmina at all during song, but merely open and close the dorsal fields, much as do the Gryllinae during courtship singing. The male coneheaded grasshopper in Plate I is not singing, but if he were, it would scarcely be noticeable from the angle that the photograph was taken. Apparently nothing that could be called a courtship song has ever been observed in Tettigoniidae, although Neoconocephalus nebrascensis has been observed to alter its song slightly when its perch was agitated slightly, such as might be done by a female approaching. In some species the females are capable of sound production by structures not at all homologous with those found in the males (Fulton, 1933, 6). In addition to the "cricket-like" copulation mentioned above for Tettigoniidae, end-to-end copulation has been observed in the Gryllacrididae (Ceuthophilus) by Turner (1915, 26), and was said by him (1916, 26) to be the "fairly constant mode of copulation" in the Tettigoniidae. In describing the copulation of Ceuthophilus latens, he says that "both animals stand upright, facing in opposite directions, while the end of the abdomen of the male is inverted and grasps that of the female by the subgenital plate." Isely (1941, 6) describes copulation in several species of Tettigoniidae in which the male backs under the female and seizes her hear the base of the ovipositor with his forceps-like cerci.

Baumgartner's work on the copulatory behavior of Gryllotalpa should be mentioned here. He found that copulation occurs in the burrows in an end-to-end position with the male lying on his back. This is the same copulatory position reported by Fulton (1924, 26) for the European Earwig, Forficula auricularia Linn., when it is in crevices. The male clings to one surface and the female to the other. When not in crevices these insects copulate end-to-end with the male rotating his abdomen so as to apply its ventral surface to the ventral surface of the female's abdomen. This would be approximately the same position assumed by the Gryllacrididae.

Various species of the singing Tettigoniidae and Gryllidae exhibit a type of behavior which I have referred to as social stimulation or acoustical stimulation. In addition to the conditions of light intensity and/or temperature and humidity which normally stimulate the males of a given species to begin their calling song, there is also acoustical stimulation between individuals. That is, the beginning of song by one individual in a colony stimulates his neighbors to song also. The alternation and synchronization of song in many species (Fulton, 1934, 6) is probably a refinement of this response. These responses exist in both the Tettigoniidae and Gryllidae, and may be described as increasing the total intensity of the sound of a colony without obscuring the specific rhythm of the song. This was very clearly illustrated in the mountains of West Virginia where tremendous numbers of the northern true katydid, Pterophylla camellifolia camellifolia, were heard singing along the highway. The sound pulsated so regularly in intensity that I thought at first the individuals were synchronising their songs, although this is normally an "alternating" species. A recording of the sound was made by sweeping the parabolic reflector in a slow arc, and when this recording was played back later in the laboratory it became clear that the pulsations in the whole sound were occurring at twice the chirp rate of a single individual. Thus this could be described as a "synchronised alternation."

From the above considerations we can deduce that the common ancestor of the Tettigoniidae and Gryllidae had similar or identical forewings, may have been either "right-winged" or "left-winged", probably produced non-musical or noise-like sounds, including a calling song, a courtship song, and possibly a fight sound of some sort. The male had dorsal female-attractive glands, and the female mounted the male in copulation, under his lifted tegmina. The males were probably somewhat sedentary, spaced themselves in the field, and may have alternated or synchronized their songs, or at least were probably stimulated to song by hearing the sounds of their neighbors. The females were "rovers," attracted by the calling songs of the males.

The most noticeable characteristic of the songs of modern Orthoptera is their wide variety of rhythms. Due to our ability to accurately analyze and portray the structure of these sounds, using tape recordings and Vibragrams, it is possible to carry our speculations concerning the evolution of sound production into the realm of how these various rhythms have developed and what were the probable characteristics of primitive orthopteran sounds.

There are two basic patterns of rhythm in orthopteran sounds. They may consist of continuous vibrations of the tegmina for indefinite periods of time, producing unbroken trills or buzzes (Plates XXXVI, XLI, and XLVIII), or they may consist of various kinds of groupings of wingstrokes (Plates XXXIII, XXXVII, XLIII-XLVII, LII, and LV). In some cases one or more groupings may be imposed on one another, producing complex patterns (Plates XLV and LV).

It seems natural to think of a more or less continuous trill as being the primitive rhythm in orthopteran sounds. Here again, however, we can get a clue by comparing the roaches and the tree crickets. As mentioned earlier, the roaches sometimes vibrate their tegmina during courtship much as do the tree crickets, but producing only a slight rustle since no specialized structures occur on the tegmina. This vibration of the tegmina occurs in short bursts of irregular length and spacing in both roach and tree cricket courtship. If we study the calling songs of tree crickets (Plates XXXVII and XXXIX), we notice two kinds of trills, in addition to the chirping song of Oecanthus niveus. Several species, such as O. nigricornis, O. quadripunctatus, O. argentinus, O. pini, and O. latipennis trill continuously. Three species, O. angustipennis, O. exclamationis, and N. bipunctata trill in short bursts of somewhat irregular length and spacing. It has already been suggested that the primitive orthopteran's first significant sounds were probably in a courtship sequence. The courtship sounds of the continuously trilling species of tree crickets (observed in O. quadripunctatus and O. argentinus) are composed of short bursts of irregular length and spacing, similar to the calling songs of the three species mentioned above. It seems likely that this same type of rhythm, almost a lack of rhythm, was employed in the sounds made by primitive orthopterans.

Two kinds of continuous trills occur in Orthoptera, with respect to the type of wing motion involved. In the type illustrated above in many species of Oecanthus, Nemobius, Trigonidiinae, Neoconocephalinae, and Conocephalinae, the wing motion consists of "open-close-open-close-open-close, etc.," with the sound made either as the wings are closed, or both during the opening and the closing. This produces a continuous trill or buzz in which the sound pulses and the intervals between them are about the same length.

In another type of trill, illustrated by the songs of Nemobius fasciatus and N. tinnulus (PlateXXXV), the fast-tinkling form of Anaxipha exigua (Plate XLI), Microcentrum rhombifolium (Plate,XLVI), and Scudderia furcata, the wing motion involved is "open-close-hold-open-close-hold-open-close-hold, etc." Here the wings are held still for intervals of varying length between strokes, and although the rate of wingstroke may be slower, the actual speed of wing motion may be the same. This type of trill probably developed from the "open-close-open-close" type, and its extreme is exemplified in species such as Microcentrum rhombifolium which lisp, or strokes it wings once, every few seconds.

Other methods of evolution from continuously trilling songs to chirping songs are exemplified in the genus Nemobius. N. carolinus has a unique, pulsating trill. Its close relative, N. confusus, has a chirping song which consists of 1-2-second chirps or short trills of exactly the same structure as sections cut out of the continuous trill of N. carolinus, but with each of these separated by a short silent interval. The song of N. palustris is almost intermediate between these two, containing trills and intervals of varying length.

One of the trilling songs of N. carolinus has every seventh or eighth pulse de-emphasized, or softer than the others (Plate XXXVI). N. maculatus has a trilling song in which every seventh or eighth pulse is completely dropped out. It would be interesting to know if this species strokes its wings during this brief silent interval.

Chirping songs of varying regularity have developed in both Tettigoniidae and Gryllidae (Plates XXXIII, XXXVII, XLIII, XLVII, XLVIII). Some species, such as the snowy tree cricket, Oecanthus niveus, deliver their chirps with extreme regularity and constancy of rhythm; others, such as Acheta domesticus and various species of

Scudderia chirp with such irregularity that each chirp seems to be an individual unit. Steady or rhythmical chirping songs are the ones that are susceptible to the development of alternation or synchronization between neighboring individuals. These responses seem largely limited to species which do not live on the ground. Of all the chirping ground crickets, Gryllotalpa hexadactyla is the only one with a very rhythmical or steady song, and it is the only species which has such a song and does not alternate or synchronize, and the only ground-inhabiting species which sings only at night. The night-singing species are almost all tree inhabitants. In the Orthoptera there seems to be a direct correlation between living on vegetation and the development of rhythmical or regularly intermittent songs (and consequently the development of synchronization or alternation), and between living in trees or high vegetation and singing at night only.

The most complicated orthopteran sounds probably occur in the genus Amblycorypha and in the subfamily Conocephalinae. Most of the Conocephalinae alternate series of single wingstrokes with short, continuous buzzes various lengths. Some buzz continuously, but at two different speeds.

The song of Uhler's katydid (Plate XLV) represents the extreme in complexity in the songs of North American Orthoptera. It consists of three distinct phases, each of which contains at least two kinds of wingstroke pulses. There are increases and decreases in wingstroke rate, increases and decreases in intensity, and single toothstrikes produced alone. All or nearly all of these characteristics appear in every repetition of the song. It is difficult to guess how such a complicated song could arise, and what factors might be involved in the maintenance of all its individual parts.

We are now brought to the point of wondering how and what song differences arise between isolated populations of a single species, on their way, so to speak, toward becoming distinct species. There are in the singing Orthoptera a number of species and infraspecific populations that can be distinguished most completely, or only, by differences in their songs. Several kinds of relationships exist between the songs of these closely related groups. In Nemobius fasciatus and N. tinnulus, long considered to populations within a single species, the courtship song of fasciatus is almost identical to the calling song of tinnulus. A similar relationship exists between the songs of N. carolinus and N. confusus (see Plates XXXV-XXXVII).

In many closely related species, the chief difference or the only difference between songs is a difference in the rate of wing-stroke. Such differences occur in the Oecanthus nigricornis group (PlateXL), the northern and the southern forms of Pterophylla (Plate XLVII), the three song forms of Anaxipha exigua (Plate XLI shows two of these.), and four of the five closely related eastern field crickets (Acheta sp.). In closely related chirping crickets, such as some of the Acheta, the chief song difference is often in the number of pulses per chirp (Plates XXVI, XXVII).

Song differences between closely related species are often so great that their method of development can hardly be guessed. There seems to be little relationship at all between the calling songs of the two thus far morphologically indistinguishable species of *Amblycorypha rotundifolia* (Plate XLIV).

The possibility of song differences acting as behavioral isolating mechanisms between closely related species has already been discussed (pp. 15-22). The consistent appearance of large differences between the songs of closely related species would lead us to believe that such a function might exist, and this could be one of the factors explaining the wide variety of sounds produced by the different species of singing Orthoptera.

Homoptera, Cicadidae

About 28 species of cicadas occur in the United States east of the Mississippi River. Of these, 12 occur in Ohio, and the rest are largely southern. Eleven species have been recorded in this study, 9 Ohio species and 2 southern species from North Carolina, one of which is as yet unidentified.

Compared to the literature on singing Orthoptera, published accounts of the distribution, ecology, life history, and songs of eastern cicadas are extremely scanty. Except for the extensive work of Davis, and Beamer's work on the biology of Kansas Cicadidae, practically none exist. This is not due to a scarcity of cicadas, since these insects are abundant throughout eastern United States. Each town and woods has its own characteristic cicada song during the summer months, and often the particular kind of cicada sound in a town is one of the attributes by which it is best remembered by visitors, or even by life-long residents. Usually, recordings of one orthopteran song after another can be played to visitors without a flicker of recognition occurring. But when the cicada song characteristic of their home town is played, they immediately light up and exclaim, "Oh, I've heard that before!" This may occur after years of absence from the locality, as it did to me when I was first starting to learn insect sounds. It is a clear demonstration that the loud and almost constant drone of cicadas through the afternoons and evenings of July, August, and September, often leaves a much deeper impression than is suspected on the minds of persons who are only rarely consciously aware of it.

The abundance of cicadas in nature is often in direct contrast to their abundance in collections, especially in the case of the eastern species which are largely arboreal. These insects are excellent fliers, and apparently have keen eyesight, since they are almost impossible to approach. Often, practically the only way to capture a specimen is to shoot it with birdshot, or some other type of fine shot. Only 4 species have been collected during this study so that their song could be definitely correlated with the specimen. For identification of the songs of the other 6 species, I am indebted to Dr. E. S. Thomas who has studied the songs of Ohio cicadas for many years.

Another complicating factor in the study of cicadas is the length of the life cycle which, according to Beamer (1928, 14) involves several years in all Kansas Cicadidae. Nine of 11 Tibicen species studied by Beamer overwinter the first year in the egg stage, and Melampsalta calliope required 4 years to complete its life cycle. The 17-year cicada, Magicicada septendecim (Linn.), is of course an extreme in this respect.

Most of the eastern cicadas mature between July 1 and August 1, and disappear sometime in late September or early October. A few species mature in May or June, such as the 17-year cicada, Cicada hieroglyphica, Okanagana rimosa, and Melampsalta calliope, and disappear in July or August.

As shown in Plate XVIII, all the cicadas encountered in the present study sing only by day, usually in greatest numbers at dusk. One species, T. chloromera (Walker) sings more in the morning than in the afternoon, and two species, T. resonans (Walker) and T. auletes (Germar) sing only for a rather short period at dusk.

With few exceptions the eastern cicadas are strictly arboreal, and are rarely found less than 20 feet above the ground. T. chloromera commonly sings on tall weeds and bushes 4-8 feet above the ground, and Melampsalta calliope, a very tiny species, occurs on low weeds and prairie plants (Beamer, (1928, 14).

The cicadas are more difficult to maintain in laboratory cages than the singing Orthoptera, and they do not perform as readily. A number of specimens were kept in large laboratory cages during this study, but none ever sang there.

Of the 4 species captured during this study, the males of all produced a "protest" sound when captured. The only other sound recorded was that produced by "solitary" males, and presumed to either attract the females, or to cause congregation of both sexes into small areas. It was noticed that cicadas are not sedentary like the males of most singing Tettigoniidae and Gryllidae, and often they are most active and do the most flying about during the time of day when the greatest numbers are singing.

Cicada songs are generally loud, resonant, non-musical sounds, lasting from 10 seconds to over a minute, and containing pulsations of various kinds and at various speeds. Often these individual songs will be interconnected for long periods of time by low-intensity, continuous buzzing. In such cases the song might be said to be a continuous sound characterized by frequent rises in intensity accompanied by the development of pulsations or beats which die out after a few seconds and are repeated again after another interval of soft buzzing, etc. When large numbers of males are singing together, the characteristics of individual songs are usually lost, and a continuous sound results.

The distribution of cicadas can be quickly and easily plotted once their songs have been learned, and the time of day and year in which they sing is known. One of the most entertaining aspects of a cross-country trip to one who knows cicada songs is to listen to the change in songs from town to town, or woods to woods along the highways.

<u>Tibicen canicularis</u> (Walker)

The Dog-Day Cicada

This insect was heard in DuPage County, Illinois, Porter County, Indiana, and Williams and Hocking Counties, Ohio, between August 15 and September 15. It was heard at all times of day, but apparently sings more in the morning than during the afternoon. It is commonly found in dry oak-hickory woods, usually 20 feet or more above the ground. Its songs are sometimes repeated at wide intervals of several minutes, so that it is difficult to record. The song lasts 15-30 seconds, and can be heard over 100 yards. It is a high, shrill whine, reminding one of the whine of a small buzz saw. As shown in Plate LV, it is composed of steady vibrations of the tympana at a rate producing about 210 pulsations per second. There are apparently no secondary pulsations in intensity caused by opening and closing of the opercula, or raising and lowering of the abdomen.

Pierce (1948, 26) says the song of this species has a pulse rate of 184-360 per second and a frequency of 7.4 kps.

<u>Tibicen lyricen</u> (DeGeer)

The Lyrical Cicada

This insect is abundant in dry oak-hickory woods in southern and eastern Ohio. It was also heard and recorded in Dunes Park, Porter County, Indiana. It song has been heard between early July and mid-September, and it apparently sings a little more in the morning than in the afternoon. Singing males are usually quite high in trees.

The song is a steady buzzing whine lasting from 20 seconds to over a minute, and with a low-intensity buzzing continuing from one song to the next. The songs, or the louder parts of the buzzing, are usually separated by 30 seconds to a minute or more in steady singing. The sound is made by a steady vibration of the tympana, with the abdomen apparently vibrated at a rate producing about 42 pulsations per second. Each of these pulsations contains 6-8 pulsations which may represent the individual vibrations of the tympana (Plate LV).

Beamer (1928, 14) gives the seasonal song period of this species as July 13–September 18 in Kansas, and says of the song that it resembles somewhat that of _T. chloromera_ but does not have the "crescendo" of that species. Davis (1922, 14) records adults between June 21 and September 10.

Tibicen chloromera (Walker)

The Swamp Ground Cicada

This species sings from late June to mid-September at Columbus, Ohio, and definitely does most of its singing in the mornings. It is generally found on weeds, shrubs, or small trees, only a few feet from the ground. It is commonly encountered on ironweed in lowland pastures, and grassy, weedy fields along roadsides, etc.

Due to its habit of perching on low vegetation while singing, this species has been watched a little more carefully than any of the others treated here. The typical singing behavior of the males I have watched is exemplified by the actions of an individual observed singing one morning on a hillside in Hocking County, Ohio. This male alighted on a sumac bush, sang one song, flew several yards to a small tree, sang two songs, flew again to a tall weed, sang once, and flew again, this time out of sight. I have seen _chloromera_ do this on many different occasions. Often the male flies immediately upon finishing the last notes of his song. This is in direct contrast to the sedentariness of males of the singing Orthoptera. The same type of behavior was observed repeatedly in the 17-year cicada in June 1956. The individuals of this species

PLATE LV.

CICADA SONGS

Fig. 165. TIBICEN CANICULARIS

Fig. 166. TIBICEN LYRICEN

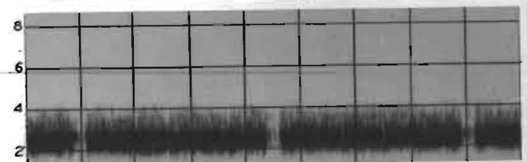


Fig. 167. TIBICEN AULETES

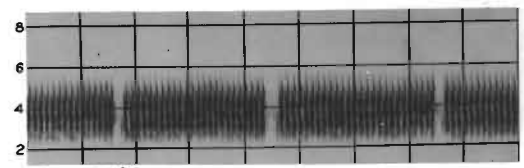


Fig. 168. TIBICEN RESONANS

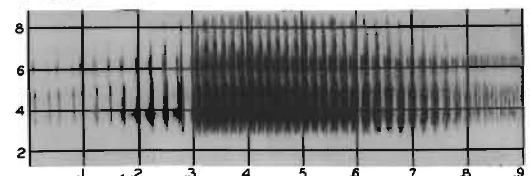


Fig. 169. TIBICEN ROBINSONIANA

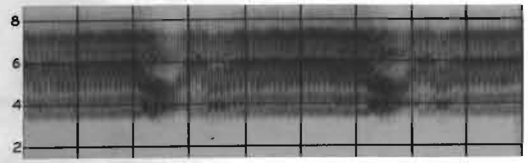


Fig. 170. TIBICEN PRUINOSA

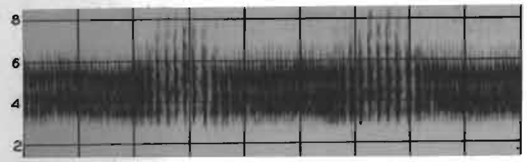


Fig. 171. TIBICEN MARGINALIS

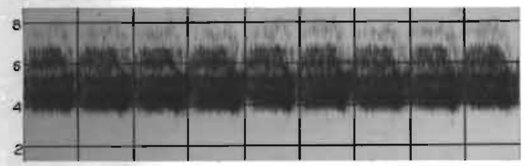


Fig. 172. TIBICEN LINNEI

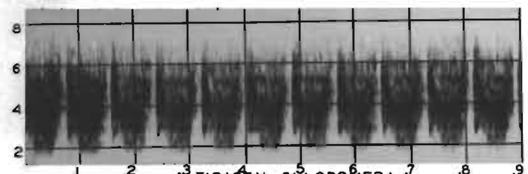


Fig. 173. TIBICEN CHLOROMERA

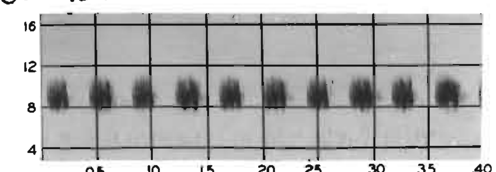


Fig. 174. OKANAGANA RIMOSA

characteristically sing 1, 2, or 3 times on each perch, then fly a short distance, perhaps only a few inches, before singing again. They begin singing immediately upon alighting, and often do not even change perches, but simply flutter the wings and leave their perch an instant between song series.

The song of chloromera is the shortest of any cicada songs recorded in this study. It lasts only 7-20 seconds, generally about 15. It is characterized by rapid pulsations in intensity apparent to the human ear (Plate LV), which are superimposed over the pulsations caused by the individual vibrations of the tympana. These secondary pulsations develop as the song increases in intensity, and eventually are delivered at a rate of about 10-15 per second. They are produced by rapid up-and-down movements of the abdomen, resulting in opening and closing of the opercula. As the song dies out, the pulsations again disappear. The interval between songs is variable, and may be only a few seconds, or several minutes. There are 15-20 vibrations of the tympana for each pulsation caused by the raising and lowering of the abdomen.

Tibicen linnei (S. and G.)

Linne's Cicada

Linne's cicada is the most abundant species in and around Columbus, Ohio. It sings between late June and mid-September from early morning until dusk, but noticeably more in late afternoon and early evening. At the Ohio State University woodlot, its daily song period overlaps with those of many of the night-singing Orthoptera (Plates XVIII, XIX).

This is a "town" species, like *pruinosa*, and I have heard "waifs" singing from utility poles in downtown Columbus, where the nearest trees were several blocks away. Singing males are scarcely ever found less than 15-20 feet above the ground. During August, large numbers of both males and females fly through open windows at night into lighted laboratories and study rooms on the Ohio State University Campus.

The song of this species and that of *chloromera* are very similar, and are often confused. Structurally they are alike, but the pulsations in the song of *linnei* are slower, 5-12 per second, and the song is longer, lasting 15-60 seconds, and only rarely shorter than 30 seconds. The tympanal vibrations occur at a rate of about 150-200 per second (Plate LV). This song is also less harsh than that of *chloromera*, and the pulsations are not so sharply separated.

Tibicen marginalis (Walker)

The Marginal Cicada

This cicada has been heard in the trees along creeks and streams from Hocking County and Ross County south to Portsmouth and Ironton, Ohio, and along the Ohio River south to Louisa, Kentucky, and in Monticello, Illinois. The earliest singing date known is August 6, though it probably matures much earlier, and the latest date songs were heard was on a trip to Ironton, Ohio, on September 4. I have collected no specimens; the song was identified by Dr. Thomas.

The marginal cicada is a daytime singer, like all the North American cicadas, and I have heard it from 10 A. M. to 5 P. M. It sings from the willows, elms, cottonwoods, sycamores, and other trees that line the stream banks in southern Ohio, generally from 20 to 30 feet above the ground when trees of this height are available.

The song of this species is rather long, lasting from 30 seconds to over a minute, and with the individual songs joined by continuous, low-intensity buzzing. The song, or perhaps more properly, the most intense, pulsating part of the song, is characterized by secondary pulsations at a rate of 2-3 per second which differ from those in the songs of other cicadas as shown in Plate LV. They actually consist of a temporary slowing of the rate of pulsations produced by the individual vibrations of the tympana, from the normal 140 per second to 50-60 per second. About 7-9 pulses are produced at this slowed rate before the normal speed is resumed for 30 or so pulses. The song interval, or the interval between the pulsating parts of the song is about 10-20 seconds in steady singing. The song is loud and can probably be heard for well over a hundred yards.

Beamer (1928, 14) says this species sings from mid-June until mid-October in Kansas, and he also says the song is seemingly identical with that of T. dealbati (Davis), "... continuous Z'we, Z'we..." "Their song begins as soon as the sun warms them in the morning and continues far into the night. Specimens have been heard as late as 1:30 o'clock in the morning."

<u>Tibicen</u> <u>pruinosa</u> Say

The Pruinose Cicada

Dr. E. S. Thomas calls this species the "Old Scissors Grinder" because of the resemblance of its song to the noise made by the scissors sharpeners used in the past by itinerant peddlers. It has been recorded in this study in Illinois, Indiana, and Ohio, and presents some variation in song in different localities that need further investigation. It is another of the "town" species, occurring in greatest numbers in residential areas of towns and cities. Like <u>linnei</u> and the snowy tree cricket, it can usually be assumed that if this species is not heard in the trees in such areas, it probably does not occur in the general locality.

Singing males are generally high in trees, and have been heard in hard and soft maple, oak, elm, and hickory. They seem to be especially abundant in areas where hard maple is present.

This species occurs over most of southern Ohio, apparently reaching northern limits in central Ohio at Circleville, Hooker, Hebron, and Zanesville. I have also heard it in Piatt, Champaign, and Vermillion Counties, Illinois, and in Fountain and Marion Counties, Indiana. In east-central Illinois this is the most abundant late summer cicada. In Fountain County, Indiana, while driving east, we noticed the song of this species rather abruptly replaced by that of <u>linnei</u>, and <u>pruinosa</u> was not heard again until a small but rather dense colony was encountered on the north side of Indianapolis along

Route 100.

In Ohio this species has been heard from mid-July until mid-September (1954). In Piatt County, Illinois, however, only a few scattered specimens remained on September 4, 1955, although the species was abundant in Piatt County on September 1, 1954. It is possible that 1954 was a brood year for the locality visited.

The song is a loud, pulsating buzz, lasting 15-30 seconds. The songs are often connected by a low-intensity, steady buzzing, and are separated by intervals of 15-25 seconds in such cases. As shown in Plate LV, the pulsations in the song of this species involve a change in pitch, or in emphasis of pitch. The rate of production of the pulses varies from one locality to the next, as does the quality of the sound. In Piatt County, Illinois, at 83° F., they were delivered at 1-1½ per second, with the dominant part of the song being the higher-pitched part, and the pulsating part of the song lasting 20-25 seconds and involving 25-30 pulsations. In Circleville, Ohio, at 75° F., the rate of pulsation was 2½-3½ per second, the emphasis was on the lower-pitched part of the song, and the songs lasted 17-28 seconds, involving 45-90 pulsations. Near Ironton, Ohio, at 92° F., the rate of pulsation was 1½-2 per second, the emphasis was on the lower-pitched part of the song, and the pulsating part of the song lasted 13-15 seconds, involving 25-31 pulsations.

Tibicen robinsoniana Davis

Robinson's Cicada

The song of this species was recorded near Lynx, Ohio (Adams County) on June 11, 1954, and in Pike County, Kentucky on August 8, 1955. It was otherwise heard August 8-11, 1955, in Russell, Glasgow, and Rockbridge Counties, Virginia, and Jackson County, West Virginia. The singing males were all over 15 feet from the ground in cedar, sycamore, cottonwood, and other trees.

The song of this species is very distinctive, a slow repetition of loud, coarse phrases, each of which builds up then dies out in intensity (Plate LV). These phrases or buzzes are repeated at a rate of about one per second, and from 20 to 40 or more are included in each song. The phrases are interconnected with each other, but this is not apparent unless one is very close to the singer. At a distance the soft intervening buzz is lost. The pulse rate due to vibration of the tympana varies from 35-40 per second to about 65 per second, this slow rate accounting for the coarseness of the sound to human ears.

Davis (1922, 14) described this song from Virginia as a "... long, drawn-out *zape*, *zape*, *zape*, continued for from one to two minutes."

Tibicen auletes (Germar)

Germar's Cicada

This cicada was recorded and collected in Hocking County, Ohio, on July 12, 1955, and recorded near Lenoir, North Carolina on August

8, 1955. In both localities this cicada was found in oak forest where it was singing from perches 15 feet or more above the ground. Like its larger southern relative, resonans, it sings only during a short period of an hour or less at dusk. This the shortest daily song period known for any singing insect. If light intensity is the major controlling factor, as seems to be the case, then apparently light above a certain intensity inhibits sound production, but a certain amount of light must be present for sound production to occur. Many species of cicadas concentrate their singing during part of the day, and most of these do so chiefly at dusk, but none are so narrowly restricted as these two species. It is difficult to speculate on the possible selective advantage of such a behavior pattern.

The song of this species lasts from 20 seconds to more than a minute and is characterized by slight breaks or "catches" occurring at rates of 2 or 3 per second. This rate changes, increasing as the song progresses, then slowing again toward the end of the song. The songs are interconnected by low-intensity continuous buzzing and occur at intervals of a few seconds to several minutes. The song is very loud and might be paraphrased, "dee-dee-dee-dee-dee-etc." As shown in Plate LV, the pulse rate caused by individual tympanal vibrations is about 150-200 per second.

Tibicen resonans (Walker)

The Resonating Cicada

This species is apparently very closely related to the preceding one, but is more southern in distribution. Recordings were made in Hart County, North Carolina, on August 10, 1955, and in Holmes County, Florida, on September 5, 1955 (Thomas Walker), both of these in oak woods at dusk. In both instances, large numbers of these insects were singing and flying about. In Florida, Walker reported (personal communication) that he was eating supper by his car at dusk in an oak forest, when he suddenly noticed a wave of noise approaching across the woods. It was so loud and was sweeping across the woods toward him so rapidly, that he thought at first it was caused by a windstorm. A moment later, however, he realized that it was the starting of song by this cicada, and a short time later, large numbers were singing and flying about all around him. The short time lapse required for this species to get into full song is probably a combination of uniform response to conditions of light intensity and a high degree of social stimulation.

The song of this species is almost identical with that described for auletes, except that the pulse rate due to tympanal vibration is about 80-90 per second, somewhat slower than the in the song of auletes, and the breaks in the song occur at a slightly more rapid rate, 3-5 per second (79° F.), as shown in Plate LV.

Okanagana rimosa (Say)

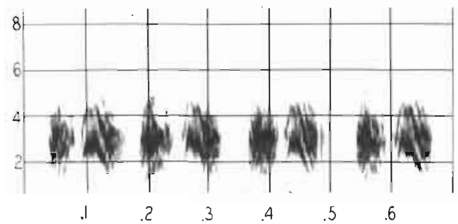
On July 26, 1955, on a sunny afternoon, an insect recording was made at Mohican State Forest, Ashland County, Ohio. The sound was a rapid, high-pitched lisping (Plate LV), much like the song of Neocono-

cephalus ensiger, but softer and higher-pitched. It was coming from high up in elm and oak trees along the park road. The singers were not seen or collected, but the song was identified as that produced by the small cicada, *Okanagana rimosa*. As shown in Plate LV, it is a continuous repeating of a high-pitched, multi-frequency note, at rates of 10-12 per second. Each note contains 8-9 pulses which may correspond to individual vibrations of the tympana. The sound is rather soft to the human ear because of its high pitch.

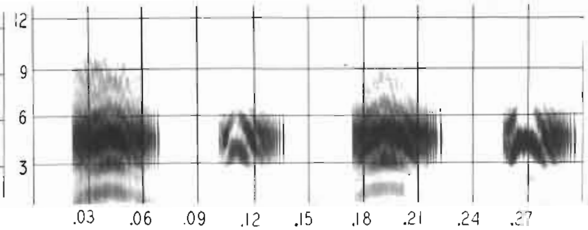
Pierce (1948, 26) records the song of *rimosa* as a "...series of trains of pulses each about 3/10 of a second long. The pulses are irregular in shape and occur at a rate of about 355 per second..." This differs considerably from the description given here, and it possible that the insect involved in the present study was *O. rimosa ohioensis* Davis.

PLATE LVI. MISCELLANEOUS INSECT SOUNDS

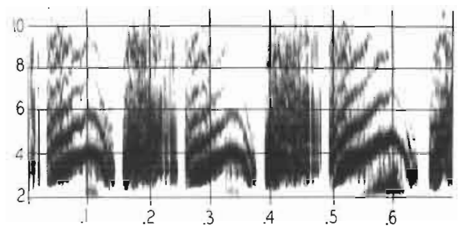
FREQUENCY IN KILOCYCLES PER SECONDS



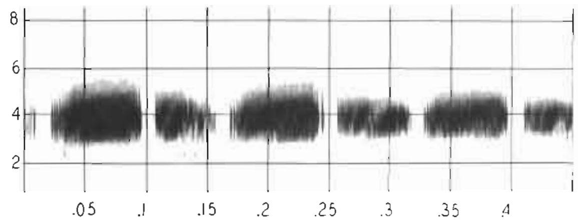
CONOTRACHELUS NENUPHAR
(COLEOPTERA:CURCULIONIDAE)
Fig. 175.



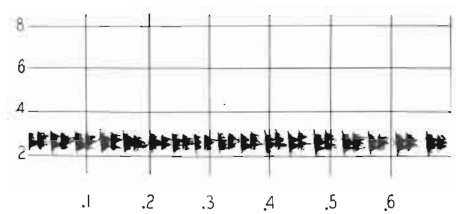
DASYMUTILLA LEPELETIERII
(HYMENOPTERA:MUTILLIDAE)
Fig. 178.



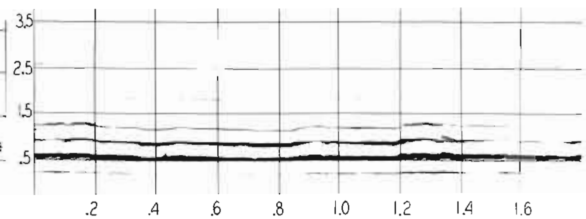
TETRAOPES FEMORATUS
(COLEOPTERA:CERAMBYCIDAE)
Fig. 176.



MELANOLESTES PICIPES
(HEMIPTERA:REDUVIIDAE)
Fig. 179.



TETRAOPES FEMORATUS
(COLEOPTERA: CERAMBYCIDAE)
Fig. 177.



PSOROPHORA CILIATA
(DIPTERA:CULICIDAE)
Fig. 180.

TIME IN SECONDS

BIBLIOGRAPHY FOR SOUND PRODUCTION AND PERCEPTION IN ARTHROPODS

Introduction

A complete bibliography for sound production and perception in arthropods would probably contain between two and three thousand references; the following contains about 1500. They are arranged alphabetically by author according to insect orders, with one section on arthropods other than insects, and one on general references, including several used in the preparation of this thesis which do not bear directly on sound production or perception. A few references are necessarily duplicated in this arrangement. However, a maximum of about 300 references occurs in each section, greatly facilitating the location of information on any particular group. In two orders, the Homoptera and the Orthoptera, certain parts of the order have been separated from the rest to avoid a few references being buried among a large number. The bibliographies on Cicadidae and Orthoptera are more incomplete than those for other groups. Sound production and perception are so universal and well-known in these groups that almost any reference on these groups is likely to have some mention of these functions. For more comprehensive general bibliographies on these groups the reader is referred to Myers (1929, 14, 1220 plus references on Cicadidae) and Blatchley (1920, 6, 700 plus references on Orthoptera). These two bibliographies, in addition to that of M. Frings (Busnel, 1954, 6), have been very helpful in making the present compilation.

No pretense is made of having examined every reference listed. In some cases there was no need to examine a reference merely to determine whether or not it should be included. Examination has been made in all cases where there is no reference to sound production or perception in the title. Many references on insect sense organs or behavior are included because it was believed that they would or should be examined by anyone initiating a study of insect sounds and behavior related to sounds. References used in the preparation of this thesis are starred.

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APPENDIX

OBSERVATIONS ON THE STARTING AND STOPPING OF SONG IN THE EVENING BY ORTHOPTERA AND CICADIDAE IN JULY AND AUGUST, 1954-55.

Introduction

On several different evenings during July and August, 1954-55, detailed notes were taken on the singing behavior of day- and night-singing species of Orthoptera and Cicadidae during the time of day that their daily singing periods were ending and beginning, respectively. These observations included the recording of light intensity, temperature, relative humidity, and time, and they lasted from 15 minutes to an hour on different occasions. They were carried out in 4 different locations: (1) a grassy clearing in the Ohio State University woodlot, about 1/6 acre in size, and almost completely surrounded by a fairly dense growth of trees 20-40 feet high, (2) along the south edge of the University woodlot, which was bordered by an alfalfa field, (3) in an isolated, apparently unsprayed apple tree on the University farm, and (4) in a vacant lot on the edge of Columbus which supported a dense colony of *Neoconocephalus ensiger*.

Methods

Light intensity was recorded with a Weston Photometer, with the sensitive element facing directly upward in the open on the ground, unless otherwise specified. Relative humidity was measured with a sling psychrometer. Temperature was measured at the height of the thermometer (12 inches) from the ground. When consecutive nightly observations were made in a particular area, the readings were taken in the same spot every night.

1. <u>Clearing in University Woods, 28 July 1955</u>

7:17 P.M., 77° F., 100% R.H., 90 Fc.* *Neoxabea bipunctata* started weak and erratic, also *Oecanthus angustipennis* (or *exclamationis*). *Tibicen linnei* still singing in large numbers.

7:25 P.M., 76° F., 100% R.H., 64 Fc. *O. niveus*, one individual gave about 12 chirps, then was silent a moment, then started steadily.

7:45 P.M., 75° F., 100% R.H., 14.5 Fc. *Microcentrum rhombifolium* started steadily.

7:52 P.M., 75° F., 100% R.H., 5.6 Fc. *Neoconocephalus nebrascensis* started steadily in weeds near west side of clearing. More individuals joined, but only after first individual had sung several buzzes — 15-20 singing eventually.

7:59 P.M., 75° F., 100% R.H., 1.7 Fc. 5 *nebrascensis* singing.

8:02 P.M., 75° F., 100% R.H., 1.7 Fc. A single 2-pulse phrase by *Scudderia curvicauda*.

8:04 P.M., 75° F., 100% R.H., 1.4 Fc. *Pterophylla camellifolia* sang a few phrases, then stopped. *T. linnei* still singing, but only a few individuals at a time.

8:10 P.M., 75° F., 100% R.H., 0.5 Fc. Last song of *linnei*.

8:13 P.M., 75° F., 100% R.H., 0.3 Fc. A single individual of *P. camellifolia* started steady singing of 2-pulse phrases, and was joined by others within a few minutes.

One *niveus* started at half speed for 4 chirps, then sang at normal speed for a few chirps, quit, and started up a few minutes later. *Nebrascensis* is definitely synchronized, that is, with about a dozen individuals singing there is always a gap between every buzz, which is silent. There is a slight lag from one individual to the

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* R.H. = Relative Humidity; Fc. = Footcandles.

next, so that each new singer starting up adds on to the end of the "collective" buzz and somewhat shortens the interval. P. camellifolia individuals are singing both 2- and 3-pulse chirps. A. oblongifolia started up later than any of the above species. All of the species discussed here began falteringly, not all at once, with the exception of N. nebrascensis.

2. Clearing in University Woods, 29 July 1955

7:10 P.M., 79° F., 93.5% R.H., 65-70 Fc. N. bipunctata weak and erratic since 7:05 P.M., 2 niveus sang a minute or two each.

7:21 P.M., 76° F., 96.5% R.H., 37 Fc. One niveus sang 60 chirps.

7:32 P.M., 75° F., 96% R.H., 30 Fc. One niveus sang 38 chirps.

7:40 P.M., 75° F., 96% R.H., 19-20 Fc. One niveus sang 78 chirps.

7:41 P.M., 75° F., 96% R.H., 18-19 Fc. One niveus sang 44 chirps.

7:43 P.M., 75° F., 95% R.H., 15-16 Fc. One niveus sang 70 chirps.

7:45 P.M., 75° F., ———, 13 Fc. One niveus sang 30-40 chirps.

7:47 P.M., 75° F., ———, 11 Fc. One niveus sang 60-70 chirps.

7:48 P.M., 75° F., ———, ——— One niveus sang 48 chirps.

7:49 P.M., 74° F., ———, 8.5 Fc. N. nebrascensis began singing in south corner of clearing; one individual began and was joined in a few seconds by others.

3. South Edge of University Woods, 29 July 1955

7:54 P.M., 75° F., 91% R.H., 6.4 Fc. Nebrascensis, niveus, linnei singing steadily.

8:00 P.M., 75° F., 91% R.H., 2.8 Fc., No linnei singing.

8:06 P.M., 75° F., 91% R.H., 1.0 Fc. No linnei singing.

8:07 P.M., 75° F., ———, 0.8 Fc. *P. camellifolia* gave a few chirps, then began steady chirping after a second or so of silence. He was joined within a few seconds by other individuals.

8:08 P.M., 75° F., ———, 0.7 Fc. One *linnei* song heard, the last one for the night.

8:09 P.M., 76° F., 91% R.H., 0.6 Fc. One *ensiger* sang a few zips, stopped for a few seconds, then sang steadily. He was quickly joined by other individuals. Just after this first *ensiger* began, a single individual of *oblongifolia* began steady chirping, and he was quickly joined by another individual who alternated chirps with him.

N. bipunctata sang steadily (at least one individual could be heard all the time) after 7:40 P.M. Often, when an individual starts, he sings the first part of his trill at a lowered speed, seemingly half speed. This is also true of *niveus*, which sometimes begins with a few chirps delivered at one-half the normal rate.

4. Clearing in University Woods, 1 August 1955

7:09 P.M., 82° F., 87% R.H., 68 Fc. *Linnei*, *O. silvaticum*, *bipunctata* singing steadily.

7:11 P.M., 82° F., 87% R.H., 58 Fc. One *niveus* sang 30 chirps.

7:13 P.M., 81° F., 87% R.H., 55 Fc. One *niveus* sang 67 chirps.

7:14 P.M., 80° F., ———, 51 Fc. One *niveus* sang 36 chirps.

7:15 P.M., 79° F., ———, 45 Fc. One *niveus* sang 7 chirps.

7:17 P.M., 79° F., ———, 43.5 Fc. One *niveus* sang 130 chirps.

7:20 P.M., 79° F., ———, 39 Fc. Two chirps by either *oblongifolia* or *curvicauda*.

7:21 P.M., 79° F., ———, 36 Fc. One *niveus* sang 140 chirps.

7:22 P.M., 79° F., ———, 35 Fc. One *niveus* sang 41 chirps.

7:24 P.M., 78° F., ———, 31 Fc. One niveus sang 17 chirps.

7:26 P.M., 78° F., ———, 28 Fc., One oblongifolia sang 3 single-pulse chirps.

7:27 P.M., 78° F., 25 Fc. One niveus sang 50 chirps, and another sang a few chirps at the same time.

7:30 P.M., 77° F., ———, 23 Fc. Three zips from south side of clearing may have been M. rhombifolium.

7:31 P.M., 77° F., ———, 21 Fc. One niveus sang 87 chirps; rhombifolium gave 3 zips, then stopped; 3 niveus singing at once, then a silent period until 7:32.

7:36 P.M., 76.5° F., ———, 19 Fc. One niveus sang 10 chirps after a silent period of 15 seconds.

7:37 P.M., 76° F., ———, 16 Fc. One niveus sang 36 chirps.

7:38 P.M., 76° F., ———, 14 Fc. One niveus sang 162 chirps and another began before he finished, and sang about 60 chirps before stopping.

7:39 P.M., 76° F., ———, 12.5 Fc. Nebrascensis began steadily, several niveus were singing, then all stopped entirely again.

5. South Edge of University Woods, 1 August 1955

7:45 P.M., 78° F., 91% R.H., 9 Fc. One ensiger sang a few zips.

7:53 P.M., 76° F., ———, 4 Fc., one rhombifolium sang 2 lisps; sang steadily for a few seconds, then stopped (ensiger).

7:59 P.M., 76° F., ———, 2 Fc. One P. camellifolia started continuously, was joined by another after a couple of chirps, and within a few seconds 3-4 individuals were singing.

8:06 P.M., 76° F., ———, 0.3 Fc. Ensiger began continuous singing; last linnei song heard just before ensiger started.

8:09 P.M., 76° F., ———, 0.15 Fc. The camellifolia male in the corner tree (heard during preceding nights) started, but didn't sing steadily until a minute or two later. The individuals singing steadily at this time are farther back in the woods.

6. <u>Clearing in University Woods, 2 August 1955</u>

7:13 P.M., 80° F., 96% R.H., 110 Fc. A few <u>bipunctata</u> singing deep in the woods.

7:15 P.M., ———, ———, 75 Fc. Only a few <u>linnei</u> singing.

7:18 P.M., 80° F., 96% R.H., 60 Fc. One <u>bipunctata</u> started along the side of the clearing.

7:20 P.M., 79° F., ———, 55 Fc. One <u>niveus</u> sang 57 chirps.

7:21 P.M., 79° F., 91% R.H., 50 Fc. One <u>niveus</u> sang 47 chirps.

7:22 P.M., 79° F., ———, 50 Fc. A single 3-pulse phrase by <u>curvicauda</u>.

7:24 P.M., 79° F., ———, 45 Fc. One <u>niveus</u> sang 230 chirps.

7:26 P.M., 78° F., ———, 40 Fc. One <u>niveus</u> sang 94 chirps, and another started before this one stopped, and sang until 7:27.

7:29 P.M., 78° F., ———, 35 Fc. The same specimen as above (presumably) sang 231 chirps before stopping.

7. <u>South Edge of University Woods, 2 August 1955</u>.

7:28 P.M., 87% R.H., 80° F., 35 Fc. One <u>niveus</u> sang 221 chirps.

7:29 P.M., 80° F., ———, 32 Fc. Another sang from deep in the woods.

7:39 P.M., 79° F., ———, 22 Fc. Three <u>niveus</u> singing at once.

7:46 P.M., 78° F., ———, 12 Fc. <u>Niveus</u> is singing continuously now; <u>nebrascensis</u> started up along the woods, then stopped after a few buzzes.

7:48 P.M., 78° F., ———, 9 Fc. <u>Nebrascensis</u> singing continuously.

7:55 P.M., 78° F., ———, 3.4 Fc. <u>Ensiger</u> started singing continuously.

7:58 P.M., 77° F., ———, 2.4 Fc. <u>Pterophylla</u> began steadily; <u>linnei</u> still singing in numbers; <u>ensiger</u> broke for a few seconds, then started up again continuously.

8:01 P.M., 77° F., ———, ———. _Linnei_ stopped, _rhombifolium_ ticking steadily.

8:05 P.M., 77° F., 87% R.H., 0.6 Fc. Three _linnei_ singing; _Pterophylla_ in corner tree started; _ensiger_ stopped an instant again.

8. _An isolated apple tree on the University Farm, 5 August 1955_

6:58 P.M., 90° F., 64% R.H., 75-100 Fc. (photometer facing straight up, then at sun). No wind, skies clear. Nothing singing.

7:10 P.M., 87° F., 64% R.H., 75-100 Fc. Nothing singing.

7:12 P.M., 86° F., 66% R.H., 70-95 Fc. Three very short trills by one _Neoxabea_, about 5 seconds apart. This sequence was repeated about 6 times, each trill lasting ½-1 second.

7:16 P.M., 85° F., 66% R.H., 55-72 Fc. Nothing singing.

7:22 P.M., 83° F., ———, 43-55 Fc. Nothing singing.

7:25 P.M., 83° F., 80% R.H., 38-44 Fc. One niveus sang 100 chirps, one _Neoxabea_ sang several trills, then silence for a few seconds, again a few trills by another _Neoxabea_.

7:30 P.M., 82° F., ———, 27-30 Fc. Several short trills by one _Neoxabea_.

7:33 P.M., 81° F., ———, 23-26 Fc. Several individuals of _Neoxabea_ singing short bursts for about 10 seconds, then silence for a few seconds, then sporadically continuous singing.

7:36 P.M., 83° F., 73% R.H., 18-20 Fc. Three _Neoxabea_ singing continuously in bursts of normal length, then back to sporadic singing again.

7:38 P.M., 84° F., ———, 14-16 Fc. _Neoxabea_ sporadically continuous.

7:40 P.M., 83° F., ———, 12-14 Fc. One _niveus_ sang 8 chirps.

7:42 P.M., 83° F., ———, 10-11 Fc. One _niveus_ sang 23 chirps.

7:43 P.M., 83° F., 9.6 Fc. One *niveus* sang 17 chirps.

7:43.5 P.M., 82° F., 9.4 Fc. One *niveus* sang 39 chirps.

7:44 P.M., 82° F., 80% R.H., 9.3 Fc. One *niveus* sang 19 chirps.

7:46 P.M., 82° F., 8.6 Fc. One niveus sang 40 chirps; several *Neoxabea* going all the time now, but still in short trill, not in "normal" song.

7:47 P.M., 81° F., 8.3 Fc. One *niveus* sang 72 chirps.

7:48 P.M., 81° F., 8.0 Fc. One *niveus* sang 61 chirps.

7:50 P.M., 81° F., 8.0 Fc. One *niveus* sang a few chirps.

7:51 P.M., 81° F., 4.3 Fc. One *niveus* sang 50 chirps.

7:53 P.M., 81° F., 3.2-3.8 Fc. 72.5% R.H. *Niveus* singing continuously; started when light was 4.0 Fc. and kept going.

9. Vacant Lot in Columbus (*Neoconocephalus ensiger*, see pp. 283-287).

Table 10

Environmental Conditions at Evening Starting of Song

by a Colony of *Neoconocephalus ensiger* (Harris)

Date	Time	Light	Temperature	Relative Humidity
26 Jul	8:05	?-1 Fc.	65-63° F.	24.5%
28	8:09	1-2	74-64	26.6
29	8:14	1-?	83-83	———
30	———	0-0	———	100.0
31	7:40	1-2	76-77	72.0
6 Aug	8:00	1-3	68-71	81.0
8	7:50	0-1	67-71	100.0
12	7:45	1-6	65-70	70.0
13	7:42	1-6	69-71	68.0

Light intensity was read in two spots, in the open (first column), and in a selected spot under the vegetation (second column), the latter presumably nearer to the actual conditions where the individuals of this species are located just prior to singing in the evening. They begin singing near the bottom of the vegetation and work upward, eventually taking a perch near the top of the vegetation. In the daytime they remain on the ground, often with the head buried in the ground cover. Temperatures were read both 3 feet above the ground (second column), and with the thermometer lying flat on the ground (first column), the latter presumably in a situation nearer to that where the insects were located.

On July 30 it was raining, and the insects did not begin singing while observations were underway, though the photometer in the open had moved to zero. Later in the evening, after the rain had slowed to a very light drizzle, the area was passed, and the insects were singing. On August 8, there was a light drizzle during the taking of readings, and the insects began singing after the light intensity had dropped below the sensitivity of the photometer down in the vegetation.

As shown in Plate XLIX, the only fairly constant factor in all these observations is light intensity. Apparently the light intensity down in the vegetation is more important than that out in the open. It should be noted that this colony always began singing almost immediately upon the starting of song by one individual. Very few "false starts" occurred, perhaps one a night, a few minutes before the first steady singing, and these "false starts" never involved more than one individual.

AUTOBIOGRAPHY

I, Richard Dale Alexander, was born near White Heath, Illinois, November 18, 1929. I received my elementary education in a country grade school, and my secondary education in the Monticello, Illinois, Community High School. I attended Blackburn College from September, 1946 to January, 1949, receiving the degree Associate in Arts in 1948. The degree Bachelor of Science in Education in Biological Science was obtained from Illinois State Normal University in 1950. From Ohio State University I received the degree Master of Science in Entomology in 1951. The next two years were spent in the Army under the military occupational specialty of Entomology Research Assistant. I served as graduate assistant in the Department of Zoology and Entomology at Ohio State University from 1950 to 1951, and from 1953 to 1955. In 1955 I received an appointment as University Fellow, which position I held for one year while completing the requirements for the degree Doctor of Philosophy.