

THE TAXONOMY OF THE FIELD CRICKETS OF THE EASTERN UNITED STATES (ORTHOPTERA: GRYLLOIDAE: ACHETA)¹

RICHARD D. ALEXANDER

Department of Zoology and Entomology, The Ohio State University, Columbus 10

INTRODUCTION

Orthopteran taxonomists are plagued with a number of genera containing species groups that defy subdivision by the time-honored criterion of morphological distinction. Although relatively few species of singing Tettigoniidae and Gryllidae have been described in the last fifty years from the eastern United States, an estimated 10 percent of the species in these groups are largely unrecognized because preserved specimens are morphologically indistinguishable. Many of these have been mentioned in the literature, and some have been recognized at one time or another as distinct species, only to be cast into synonymy or compromised as trinomials by subsequent authors. Many of them have been variously referred to as "physiological races," "ecological races," "biological races," "song forms," or by other more or less meaningless terms.

Our present knowledge of the relationships of many of these species is largely the result of the contributions of B. B. Fulton whose investigations have been characterized by field recognition of species on the basis of distributional, ecological, seasonal, and song relationships, followed by attempts to find morphological characters by which preserved specimens can be separated. Much of Fulton's work has been conducted with groups upon which supposedly exhaustive studies had already been carried out through morphological analysis of large series of preserved specimens.

However, even Fulton has hesitated to honor with formal nomenclature species which cannot be distinguished "on the pin." This stand has been supported by Hubbell (1954, 1956) and other orthopterists (personal communication), apparently on the grounds that (1) this is a relatively rare phenomenon, (2) only a small group of workers will be concerned with such situations, (3) a great deal of confusion would result if museum workers could not apply the proper specific names to specimens in their collections, and (4) in such cases the designation of the entire group by a single specific name and the use of colloquial names to distinguish the various species will suffice for most applied problems and museum collections.

The evidence indicates that the presence of morphologically indistinguishable species is not at all a rare phenomenon in the Orthoptera, and the work done by Fulton might well serve as an example for investigators puzzling over morpho-

logically ill-defined forms in the non-singing Orthoptera with distributional, ecological, and seasonal relationships analogous to those occurring between closely related species in the singing Orthoptera.

It is difficult to estimate the size of the group of workers which will be interested in a particular group of closely related species. There is a growing amount of published material dealing with the morphology, physiology, nutrition, and genetics of certain groups of Orthoptera in which the organisms involved were not and now perhaps cannot be identified because the investigator was not aware of the existence of several species in the group he was studying. Yet many morphologically ill-defined species are easy to separate when alive, in some cases even easier for the non-specialist than morphologically well-defined species, since their ecological, seasonal, and song relationships have been more thoroughly studied and are easier to interpret. If these closely related pairs and groups of species remain unknown to all but a handful of orthopterists, their potential usefulness to students of systematics and evolution will not be realized.

As with most biological phenomena, the problem of morphological distinctness is not always clear-cut. For example, if only one sex of a species can be identified, this still leaves specimens which cannot be determined. In the present study of the five species of *Acheta* in the eastern United States, certain pairs of species can always be distinguished "on the pin," at least in one sex. In others only certain percentages of the individuals can be distinguished. This paper is the first of a series concerning several such species groups whose relationships have been clarified through a study of sound production and associated behavior in the Orthoptera.

In addition to the type material of *A. fultoni*, representative male and female specimens and tape recordings of the calling songs of each of the species discussed in this paper will be deposited in the Museum of Zoology, Ann Arbor, Michigan. Representative male and female specimens will also be deposited in the United States National Museum and the Entomological Museum of The Ohio State University. An additional copy of the tape of the calling songs will be deposited with the Cornell Laboratory of Ornithology (Repository for the International Committee on Biological Acoustics). All the original recordings used for analysis are in the Library of Animal Sounds, Department of Zoology and Entomology, The Ohio State University.

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PRESENT STATUS OF AMERICAN *Acheta*

Native field crickets in the genus *Acheta* occur over most of North, Central, and South America, in the West Indies, the Galapagos, and on many other islands. Within this area they can be found almost everywhere except at high altitudes, in the far north, and in extremely moist 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, and an almost uninterrupted flow of taxonomic papers dealing with the group has continued since. Forty-seven names had been applied to the American field crickets by 1903. Lutz in 1908, and Rehn and Hebard in 1915, 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,² 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 the 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, and deserts), (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) recognized this ecological distribution of morphologically similar forms, but because no discontinuities existed with respect to the characters they observed, described them (p. 294) as "... mere variations, the adaptations of this exceedingly plastic species to local environmental conditions." They further stated (p. 299) "... 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) was the only investigator to supply detailed biological information along with description of new species. A number of workers, such as McNeill (1889) in Illinois, Allard (1929) in Georgia and New England, Severin (1935) in South Dakota, Ball (1942) in Arizona, and Cantrell (1943) 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, when the present study was begun, 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 has revealed three species in northeastern United States, one of these in addition to the four discussed by Fulton (1952), making a total of five species known in eastern United States. In view of the complexity of the situation, it is 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 AND SYNONYMY

There are forty-seven names available for American *Acheta* from descriptions based almost entirely on morphological characters (see Rehn and Hebard, 1915). For four of these descriptions the type locality given is simply "North America." Six descriptions were of specimens from western United States, and eight were of specimens from eastern United States. The rest were from Jamaica, Bermuda, the Galapagos Islands, Guadalupe Island (Lower California), and various South American countries. Fifteen types have been examined by the writer, including all but three of the possible twelve from eastern United States. Information concerning the types of the remaining three (*G. luctuosus* Serville, *G. abbreviatus* Serville, and *G. scudderianus* Saussure) was obtained through correspondence with Dr. Lucien Chopard, Paris, and Dr. Charles Ferriere, Geneva.

²The sequence of changes in the genus name used for American field crickets (*Gryllus* Linnaeus, 1758, to *Gryllulus* Uvarov, 1935, to *Acheta* Fabricius, 1775) is discussed in detail by Gurney (1950, 1951). Since completion of this manuscript the writer has been informed by Dr. Gurney (in correspondence) that Chopard (Mem. Soc. Roy. Ent. Belgique 27: 153, 1955) has suggested that the present separation of American and some other field crickets and the European house cricket in the genus *Acheta* be dropped, and that the genus name *Gryllus* again be used for all the crickets in this general group. Dr. Gurney states, "I have decided to continue using *Acheta* until going into the matter further, but I expect the changes will eventually be accepted here because the genera [*Acheta* and *Gryllus*] have been rather artificial."

In the course of this study several thousand specimens have been examined from all over the United States, and from Jamaica, Puerto Rico, Mexico, and several South American countries. The type of *A. assimilis* Fabricius (1775, Jamaica) has been lost, according to Dr. S. L. Tuxen, Copenhagen, where the Fabricius collection is on

loan from the Zoological Museum at Kiel, Germany. This information has been confirmed by Dr. Tischler at Kiel. Specimens obtained from Jamaica through the kindness of Mr. Thomas Farr of the Science Institute at Kingston appear morphologically distinct from all the species discussed here, and Fabricius' description is so brief that it could be applied to almost any of the American species. From morphological comparisons alone it seems unlikely that any of our eastern species extend into Central or South America.

The types of the following species described from western United States have been seen by the writer: *G. personatus* Uhler, 1864, Kansas; *G. vocalis* Scudder, 1901, Palm Springs and Los Angeles, California; *G. integer* Scudder, 1901, West Berkeley to San Diego, California; *G. armatus* Scudder, 1902, Beaver Dam, Utah, Ehrenberg and Fort Whipple, Arizona; and *G. alogus* Rehn, 1902, Albuquerque, New Mexico. The type of the only other species described from this area, *G. lineaticeps* Stål, 1858, San Francisco, California, has been lost, according to Dr. R. Malaise of the Natural History Museum, Stockholm. *G. personatus* Uhler is quite distinct from all the eastern species, and seems to be recognizable in collections. Even Rehn and Hebard recognized the distinctiveness of this form, stating (1915, p. 294), that it "... constitutes the nearest approach to a geographic racial development." The taxonomic status of the other five species is not yet clear, but any that are the same as an eastern species here recognized are synonyms of a species described earlier; hence none of these western names need be considered as valid names of any of the eastern species. The synonymy which is given below is based on distribution, morphology, and life history, and discussions of the reasons for the less evident decisions will be found in the sections treating these characteristics.

Acheta pennsylvanica (Burmeister)

NORTHERN FIELD CRICKET

Gryllus pennsylvanicus Burmeister, 1838, p. 734, North America; Zoologisches Museum, Humboldt-Universität zu Berlin (male lectotype here designated from syntypes; only labels are type label, catalogue number 983 (same as for other specimens in series), and determination labels as follows: *pennsylvanicus* Burm.*, *abbreviatus* Serv., *pensylv.* Timerm., *Gryllus* L. Burm.).

Gryllus luctuosus Serville, 1839, p. 335, North America; Museum National d'Histoire Naturelle, Paris (only a single female remains).

Gryllus abbreviatus Serville, 1839, p. 336, North America; Museum National d'Histoire Naturelle, Paris (only a single female with broken ovipositor remains).

Acheta nigra Harris, 1841, p. 123, no type locality given, but apparently New England; Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts (type probably destroyed; a few remnants of two specimens, a male and a female, remain, and an entry in Harris' notebook, "Autumn of 1834," indicates these specimens were from a fall population which would preclude their being any species other than *pennsylvanicus*).

Gryllus angustus Scudder, 1862, p. 427, Cambridge and Cape Cod, Massachusetts; Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts.

Gryllus neglectus Scudder, 1862, p. 428, Massachusetts and Cape Cod, Massachusetts; Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts.

Gryllus arenaceus Blatchley, 1903, p. 434, sand dune region of Lake County, Indiana; Entomological Collection, Purdue University, Lafayette, Indiana.

Acheta firma (Scudder)

BEACH CRICKET (Fulton, 1952)

Gryllus firmus Scudder, 1902, p. 294, Brookville, Indiana, Smithville and Pungo (not Dingo) Bluff, North Carolina; Georgia; Sanford and Key West, Florida; Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts. Lectotype here designated, male from Pungo Bluff, North Carolina. Scudder's Brookville, Indiana, specimen is *Acheta pennsylvanica* (Burmeister).

Acheta rubens (Scudder)

TRILLER FIELD CRICKET (Fulton, 1952)

Gryllus rubens Scudder, 1902, p. 294, Auburn, Alabama; Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts (description based on a single female).

Acheta vernalis (Blatchley)

NORTHERN WOOD CRICKET

Gryllus assimilis vernalis Blatchley, 1920, p. 704 (nom. nov.). Although Blatchley's holotype and allotype female, both from Crawford County, Indiana, are of this species, some of the specimens in his collection which he determined as *vernalis* are *A. fultoni* n. sp., described below.

Gryllus americanus Blatchley, 1903 (not Drury, 1773), p. 443, Crawford, Posey, Vigo, Putnam, Marion, Marshall, Wells, and Lake Counties, Indiana; Entomological Collection, Purdue University, Lafayette, Indiana.

Acheta fultoni n. sp.

SOUTHERN WOOD CRICKET

Holotype Male: Collected by the author in Hocking County, Ohio, Goodhope Township, Section 18, 4 June 1955, in a patch of leaf litter just outside an oak forest bordering an abandoned hillside field dominated by *Andropogon virginicus* L. Head, pronotum, and abdomen black; tegmina and cerci a rather uniform light brown; hind femora and all tibiae and tarsi a dull reddish. Pronotum narrowest near its anterior border; head narrower than pronotum; tegmina reaching to base of cerci; underwings completely hidden by tegmina. Otherwise not distinguishable from other American *Acheta* except by body measurements given below, and as shown in Figures 1-6, 16, and 17.

Allotype Female: Collected with holotype; same as holotype except tegmina lack reaching to base of cerci by about four abdominal segments; ovipositor reddish brown, darker near the base.

Measurements of Holotype and Allotype (in millimeters, made with ocular micrometer in binocular microscope): Body length, ♂, 15.8, ♀, 16.4; pronotal length, ♂, 3.5, ♀, 3.5; pronotal width, ♂, 5.2, ♀, 5.2; head width, ♂, 4.3, ♀,

4.3; length of hind femur, ♂, 10.3, ♀ 10.6; length of tegmina, ♂, 8.3, ♀, 9.0; length of ovipositor, 12.0.

Paratypes: Alexander Collection (collected by the author unless otherwise indicated: OHIO: type locality, 12 May 1954, 1♂ (E. L. Sleeper); 28 June 1954, 5♂; 4 June 1955, 26♂, 7♀; Fairfield Co., Madison Twp., Section 2, 5 June 1955, 2♂; 12 May 1955, 2♂; Adams Co., Jefferson Twp., Cedar School, 8 June 1955, 1♂. ILLINOIS: Jackson Co., about one mile south-east of Carbondale, 15 June 1955, 1♂; Giant City State Park, Jackson Co., 15 June 1955, 8♂, 3♀; Wolf Lake, Union Co., 15 June 1955, 3♂, 1♀.

form, especially the distinctively narrow, retracted appearance of the head and the anterior narrowness of the pronotum is very similar to that of *vernalis*. Specimens from North Carolina, where this species occurs in pine-deciduous forests and along their borders, average larger and darker than those from Ohio and Illinois, where the species occurs in *Andropogon*-covered hillsides and along the borders of oak forests around such fields.

The life history, ecology, and general morphological characteristics of the southern wood cricket in North Carolina were described by Fulton (1952). This species is named in honor

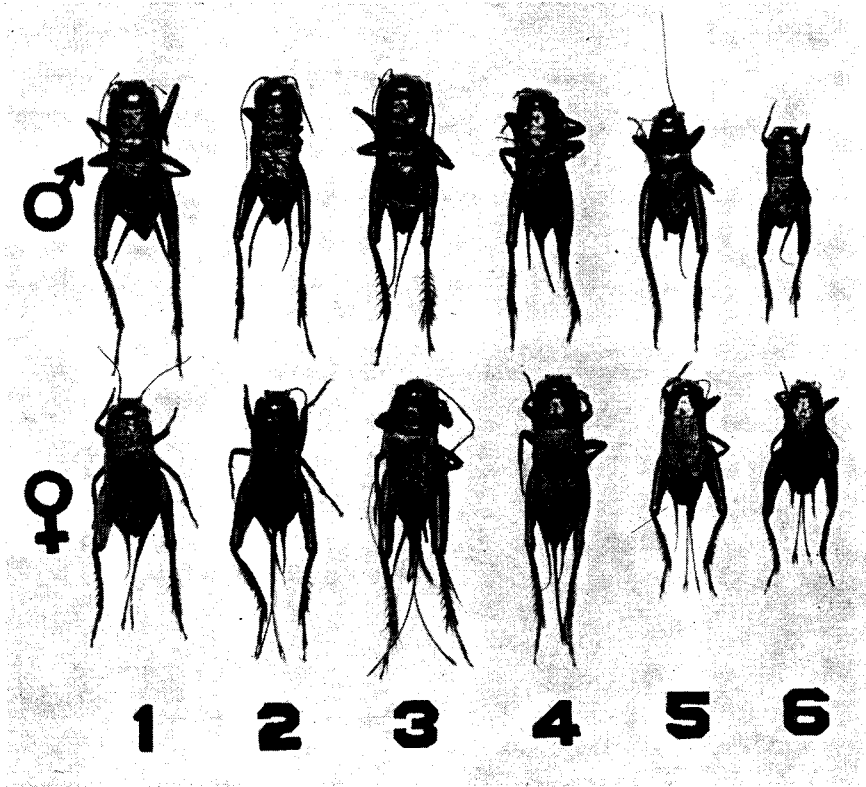


FIG. 1-6. Photographs of typical adult specimens of eastern field crickets. 1, *Acheta pennsylvanica* (Burmeister), spring brood; 2, *A. pennsylvanica* (Burmeister), fall brood; 3, *A. firma* (Scudder); 4, *A. rubens* (Scudder); 5, *A. fulltoni* n. sp.; 6, *A. vernalis* (Blatchley). X 0.94.

MARYLAND: Snow Hill, Worcester Co., 21 July 1956, 1♂; Whiton, Worcester Co., 21 July 1956, 1♂. NORTH CAROLINA (B. B. Fulton): Raleigh, 27 May 1929, 1♀; 3 June 1931, 1♂, 1♀.

This species is closest to *Acheta vernalis* (Blatchley) from which it differs in being slightly larger and in having brown tegmina and reddish appendages (at the least having reddish markings on the hind femora and usually on other appendages). As shown in figures 17 and 18, the tegmina in the male and the ovipositor in the female are both slightly longer in proportion to body length than in *vernalis*. The general body

of Dr. Fulton, whose keen investigations first aroused the interest of the writer in the singing Orthoptera, and whose prompt and excellent replies to correspondence, and expert aid in locating and collecting singing Orthoptera have been invaluable in this and other studies.

The lack of understanding of American field crickets by early investigators is perhaps best revealed by the fact that an eastern species remains today to which none of the existing names, shuffled and reshuffled many times, seems to apply. This species was apparently first recognized by Fulton (1952) who called it the "wood

cricket." The only earlier literature reference which seems to apply to this form is a remark by Rehn and Hebard (1915, p. 302) under the morphological class for which they include the names *luctuosus* Serville and *abbreviatus* Serville. They state, "The maximum of this [morphological] condition is found in material from the pine woods of southeastern United States." However, most of the specimens in the series determined by Rehn and Hebard as representative of this class are probably *rubens*. Furthermore, since field-collected specimens of this species never have the underwings exceeding the tegmina, and the single remaining female of *luctuosus* in Serville's collection is long-winged, this name could not apply. The measurements given for both *abbreviatus* and *luctuosus*, in addition to the almost solid black coloration, probably preclude their being any species but *pennsylvanica*. In correspondence, Dr. Lucien Chopard states, "I think that *abbreviatus* is the micropterous condition of *luctuosus*; both are very close to *pennsylvanicus*."

Only one name which could have been applied to a field cricket occurring in the eastern United States, *Gryllus scudderianus* Saussure, 1874, is omitted from the above synonymy. Saussure described eight species of field crickets and gave Mexico or various South American countries as type localities for all except this species, for which he gave only North America. Furthermore he named this species after Scudder, who did practically all his work on this group within the United States. In his discussion of the American species of *Gryllus*, Saussure placed *scudderianus* between *pennsylvanicus* Burmeister and *mexicanus* Saussure. In 1877 he placed *scudderianus*, along with *neglectus*, as a synonym of *abbreviatus* Serville. He described *scudderianus* from a male and a female, but according to Dr. Charles Fierriere, only a single female remains in the collection in the Natural History Museum, Geneva, Switzerland, with "Amer. Sept." and "Mr. H. deSaussure" the only information on the label. There is no indication as to how or where Saussure obtained this specimen. In general, the measurements Saussure gave for the type specimens fall somewhere near those obtained for specimens of *vernalis* and *fulloni* in the present study (body length, ♂, 14 mm., ♀, 15.0; ovipositor length, 15.0 mm.). Since both type specimens had brown tegmina and hind femora, it cannot be the same as *vernalis*. Practically all the available measurements differ from those given here for *fulloni*, and especially noticeable is the variation in proportionate length of body and ovipositor. It seems most probable that if Saussure's types came from eastern United States (and this is certainly doubtful), they represent dwarfed, atypical specimens of *pennsylvanica* (Burmeister), or *rubens* (Scudder). Very small specimens of these species have been seen, which nevertheless retain the general body proportions

and other characteristics of the typical larger specimens. However, the deviation of *scudderianus* from the measurements given for species treated here, and the improbability of discovering further information about this name, in the opinion of the writer, justifies its exclusion from the present discussion.

DISTRIBUTIONAL RELATIONSHIPS

The known distribution of the eastern field crickets, based almost entirely on the collections and "listening" records of Fulton and the writer, is shown in figure 7. The Missouri, Arkansas, Louisiana, and Mississippi records were obtained by Thomas J. Walker on a trip through this area, June 14-17, 1956. The Fentress and Cumberland County, Tennessee records for *vernalis* are from specimens in the University of Michigan Museum of Zoology collected by T. H. Hubbell on July 19, 1924, and July 13, 1922, respectively. The Fentress County, Tennessee, and Fulton County, Georgia records for *fulloni* are from specimens in the University of Michigan Museum of Zoology collected by T. H. Hubbell on June 10, 1925, and April 28, 1938, respectively. The Quantico, Virginia record for *fulloni* is from specimens in the Ohio State Museum collected by Edward S. Thomas on May 25, 1935. The general lack of records in the Kentucky-Tennessee-Alabama area is due to a lack of collecting in that area.

The most complete portions of the records are in the northward extension of *rubens*, the southward extension of *pennsylvanica*, the northward extension of *fulloni* in Ohio and on the Delaware peninsula, and the northward extension of *firma* along the Atlantic coast. The western limits are not known for any of the species. The northward and southward extensions of *vernalis* are not known. However, all of the 740 plus specimens from Michigan in the collection at Ann Arbor are *pennsylvanica*, and no specimens of *vernalis* have been found among hundreds of specimens seen from Wisconsin, Minnesota, Canada, and the New England states.

To avoid the possibility of error, distribution records based only on specimens seen in collections have not been included for *pennsylvanica*, *rubens*, or *firma*. The morphological variability and overlap of the specimens which would be referred to these three species suggests at least the possibility that additional species not encountered in this study may occur in eastern United States. Consequently, for all specimens determined as belonging to one of these three species, either the habitat or the song is known, in addition to the collection date and locality.

ECOLOGICAL RELATIONSHIPS

A. pennsylvanica occurs in all kinds of grassy situations, such as fields, pastures, weedy areas, roadsides, and lawns, and it is the most abundant and continuously distributed field cricket in

northeastern United States. In southeastern United States it is replaced in similar situations by *rubens*. These are probably the only field crickets in eastern United States which occur in

appropriate places and achieve sufficient abundance to become economic pests. They are also much easier to collect than any of the other species, and therefore dominate collections of

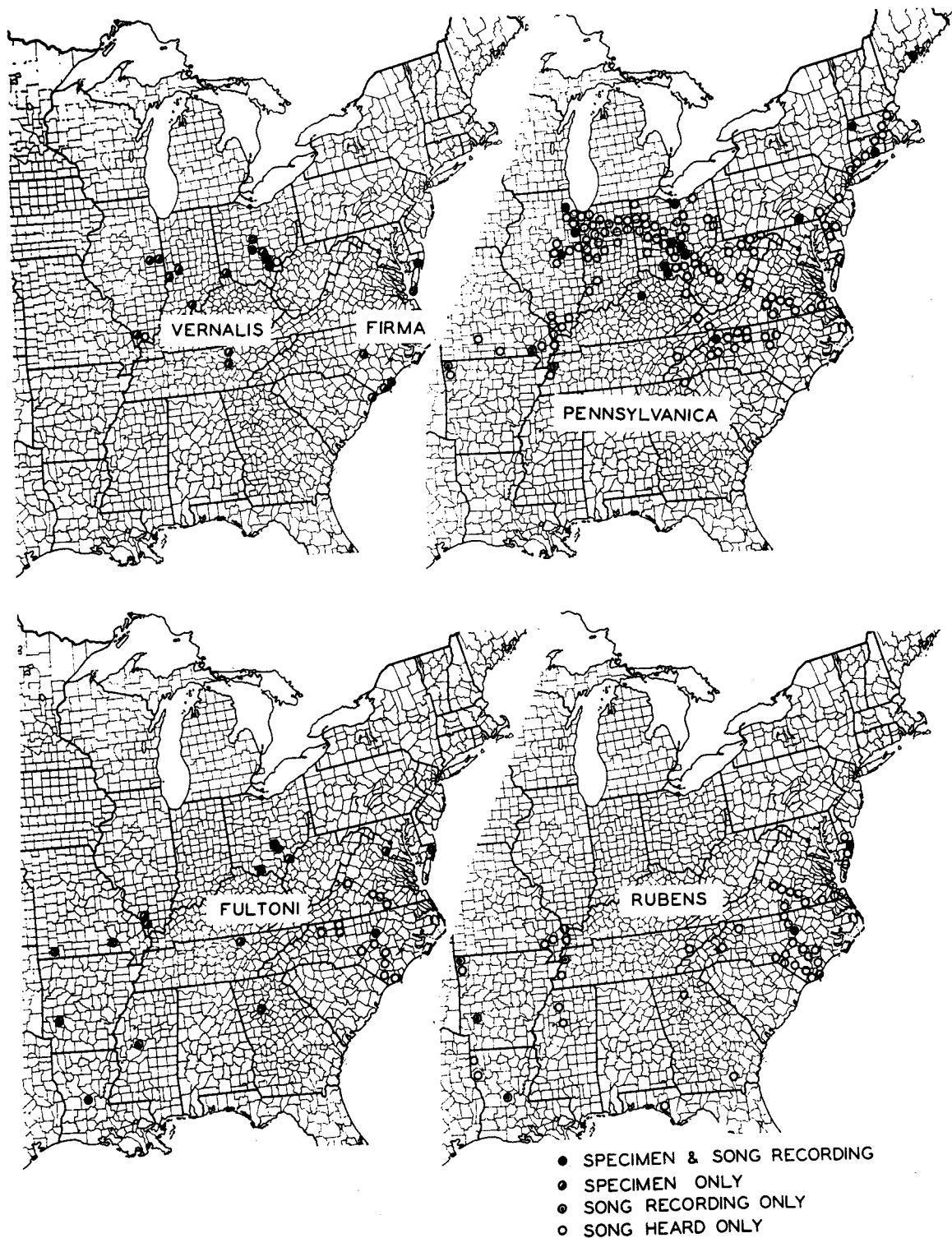


FIG. 7. Distribution of eastern field crickets.

eastern *Acheta*. This is perhaps one of the most important reasons for the confusion in early attempts to split this genus into species on the basis of morphological characters. Lutz (1908) 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 (p. 6), "Typical specimens of *americanus* [*vernalis*] and *firmus* 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 likeli-

Fulton found chirping crickets in inland sand hills in Harnett and Hoke Counties, North Carolina, which produced fertile offspring in crosses with ocean beach crickets (personal communication). Audiospectrographic analysis has shown these island specimens to have the same song as the ocean beach crickets.

The distribution of *firma* along the Gulf coast and inland in that area is unknown. However, crickets morphologically resembling beach crickets have been seen in collections from inland locations in Mississippi, Alabama, and Georgia. Light-colored crickets occur in sandy areas

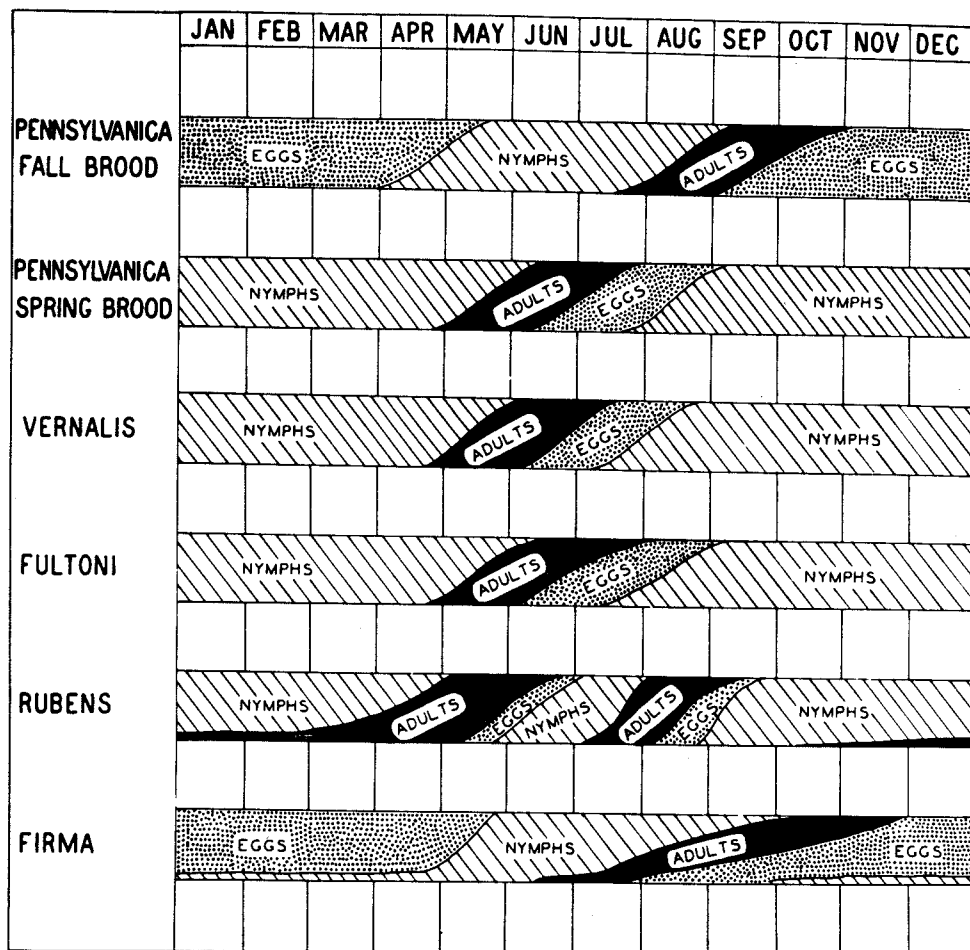


FIG. 8. Seasonal life histories of eastern field crickets.

hood of encountering them and greater difficulty in capturing them. Of approximately 2700 eastern field crickets examined in six collections in eastern United States, there were about 1900 *pennsylvanica*, about 750 *rubens* and *firma* combined, 72 *vernalis*, and 24 *fulltoni*. This does not include the collections of Fulton and the writer.

As stated by Fulton (1952, p. 285), *firma* inhabits "the flat sandy area bordering the ocean beaches. This may be grassy or shrubby or largely bare sand, but is not wooded." Later

around Lake Michigan and Lake Erie, along the Illinois and Mississippi Rivers, and probably in similar areas all over eastern United States. Such specimens were responsible for Blatchley's description of *arenaceous* from Lake County, Indiana. However, crossing experiments and song analysis have revealed light-colored specimens collected at Dunes State Park, Indiana, along Lake Michigan, and Cedar Point, Ohio, along Lake Erie, to be conspecific with the more commonly encountered, darker-colored specimens

of *pennsylvanica*. Such specimens apparently represent "adaptations . . . to local environmental conditions," such as are referred to by Rehn and Hebard (1915, p. 294). The morphological variants from inland localities in Mississippi, Alabama, and Georgia, however, remain to be checked, and may represent additional species to those discussed here.

A. vernalis is found in leaf litter in deciduous

forests. In North Carolina and Virginia, where *vernalis* does not occur, this habitat is occupied by *fultoni*, which is abundant in deciduous and pine-deciduous forests, and along the forest borders. Both *vernalis* and *fultoni* occur in southern Ohio, Indiana, and Illinois. Here, however, *fultoni* is chiefly an inhabitant of dry, *Andropogon*-covered hillsides. In southeastern Ohio it is found almost exclusively in old fields, 10 to 30 years

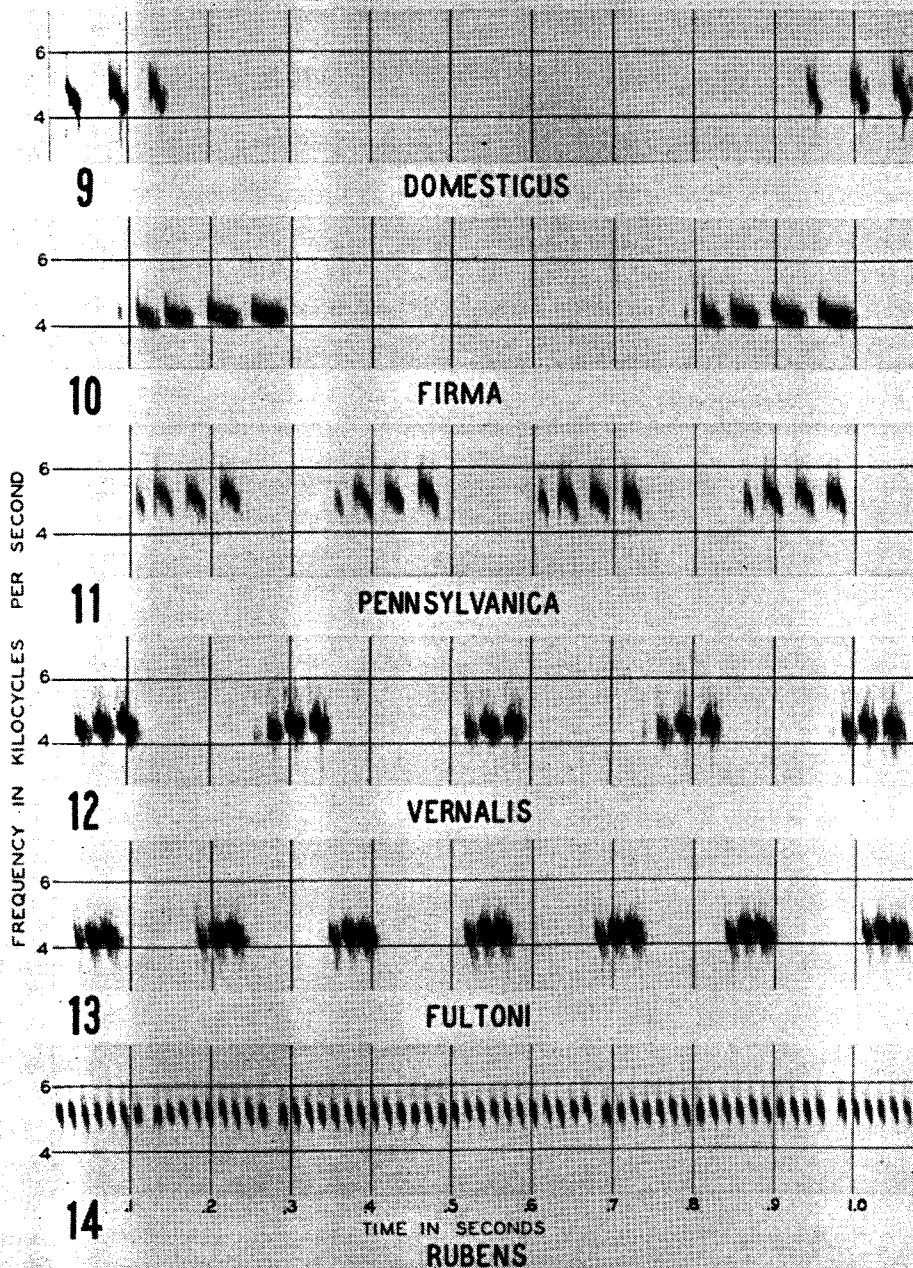


FIG. 9-14. Sample audiospectrographs of typical calling songs of *Acheta* species. 9, *Acheta domestica* (Linnaeus); 10, *A. firma* (Scudder); 11, *A. pennsylvanica* (Burmeister), spring brood; 12, *A. vernalis* (Blatchley); 13, *A. fultoni* n. sp.; 14, *A. rubens* (Scudder).

abandoned, which are dominated by *Andropogon virginicus* L. In southwestern Ohio and west to along the Mississippi River bluffs in southern Illinois, *fultoni* occurs in the hilltop prairie openings dominated by *Andropogon scoparius* Michx. In both Illinois and Ohio, *fultoni* is often more abundant along the forest borders around such fields than it is out in the fields themselves. In Maryland, Virginia, Arkansas, and Missouri, *fultoni* has been found both in *Andropogon* fields (and similar grassy areas) and in leaf litter in woods. The factors involved in this ecological variation remain to be elucidated. However, morphological comparisons, song analyses, and a single successful crossing experiment (between an Ohio female and a North Carolina male) seem to indicate that a single species is involved, with geographic variation in habitat and in certain song characteristics which will be described later.

A. fultoni and *pennsylvanica* overlap but little with *vernalis* where their habitats meet in Ohio. On the other hand, *fultoni* and *pennsylvanica* occur together in the same fields in southern Ohio, and appear to be randomly intermixed in such areas. *A. rubens* and *firma* have been found in mixed colonies at Kure Beach and Carolina Beach, North Carolina. In Worcester County, Maryland, *rubens*, *firma*, and *fultoni* were found together along the border of a wheat field, and *pennsylvanica* was collected only a few yards away along a grassy roadside.

SEASONAL LIFE HISTORIES

The seasonal relationships of the eastern field crickets are indicated in figure 8. The diagrams for *rubens* and *firma* are redrawn from Fulton (1952). *A. fultoni* has approximately the same life history in North Carolina as in Ohio.

No way of distinguishing the spring and fall broods of *pennsylvanica* in Ohio has been found other than the differences in their life histories, and a slight difference in the relative length of the body and the ovipositor in most females (fig. 18). One brood overwinters as partly grown nymphs, one or two instars from adulthood, and produces adults which sing from early May until about mid-July. The other overwinters in the egg stage and produces adults which sing from mid-July until frost. These two broods occupy the same habitat, a fall male often moving into the same burrow or niche inhabited by a spring male earlier in the season. There is a slight overlap of adults in mid-July. Although very few adults can be seen or heard at this time, there were at least a few singing males on the Ohio State University campus every night from May to October during the three years of this study. The end of the spring brood and the beginning of the fall brood are difficult to determine, but are indicated by the gradual disappearance of singing males in familiar locations, and the appearance of

numbers of singers in new locations. Adult male field crickets are sedentary, ordinarily remaining in and singing from the same location throughout their adult lives.

There are indications that offspring of the spring brood of *pennsylvanica* never mature in fall in Ohio. No adults or last instar nymphs have ever been taken in early winter. Last instar nymphs of the fall brood can be found on the Ohio State University Campus until mid-September, but later in the fall only adults of the fall brood and young nymphs of the spring brood, 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 this group 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. Neither *fultoni* nor *vernalis* mature in the fall in Ohio, but both produced offspring from early May matings in the laboratory which began maturing in mid-August and early September, respectively. Several factors may be involved in these discrepancies between field and laboratory observations, such as temperature, diet, photoperiod, and water availability.

Fulton's findings in North Carolina indicated that offspring of spring adults of *pennsylvanica* may sometimes mature in the fall, while Cantrall (1943) failed to obtain any fall adults from seven pairs of spring brood adults caged outside on June 9, in Michigan. On the George Reserve, Michigan, only about five percent of the total number are spring crickets, a result, Cantrall believes, of high mortality among overwintering nymphs. In central Ohio, no noticeable difference in numbers occurs between the spring and fall broods. These two broods may interbreed in mid-summer, or possibly in fall in the southern part of their range, 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.

A. vernalis and *fultoni* overwinter as nymphs one or two instars from adulthood, and during the three seasons that this study has been in progress, they have matured a week or two earlier than *pennsylvanica* in southern Ohio, beginning to sing in late April or early May. The adults disappear in late July and early August. In North Carolina, Fulton (1952) says *fultoni* sings from mid-April until early August. The 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 female from Hocking County, Ohio, on August 18, and was

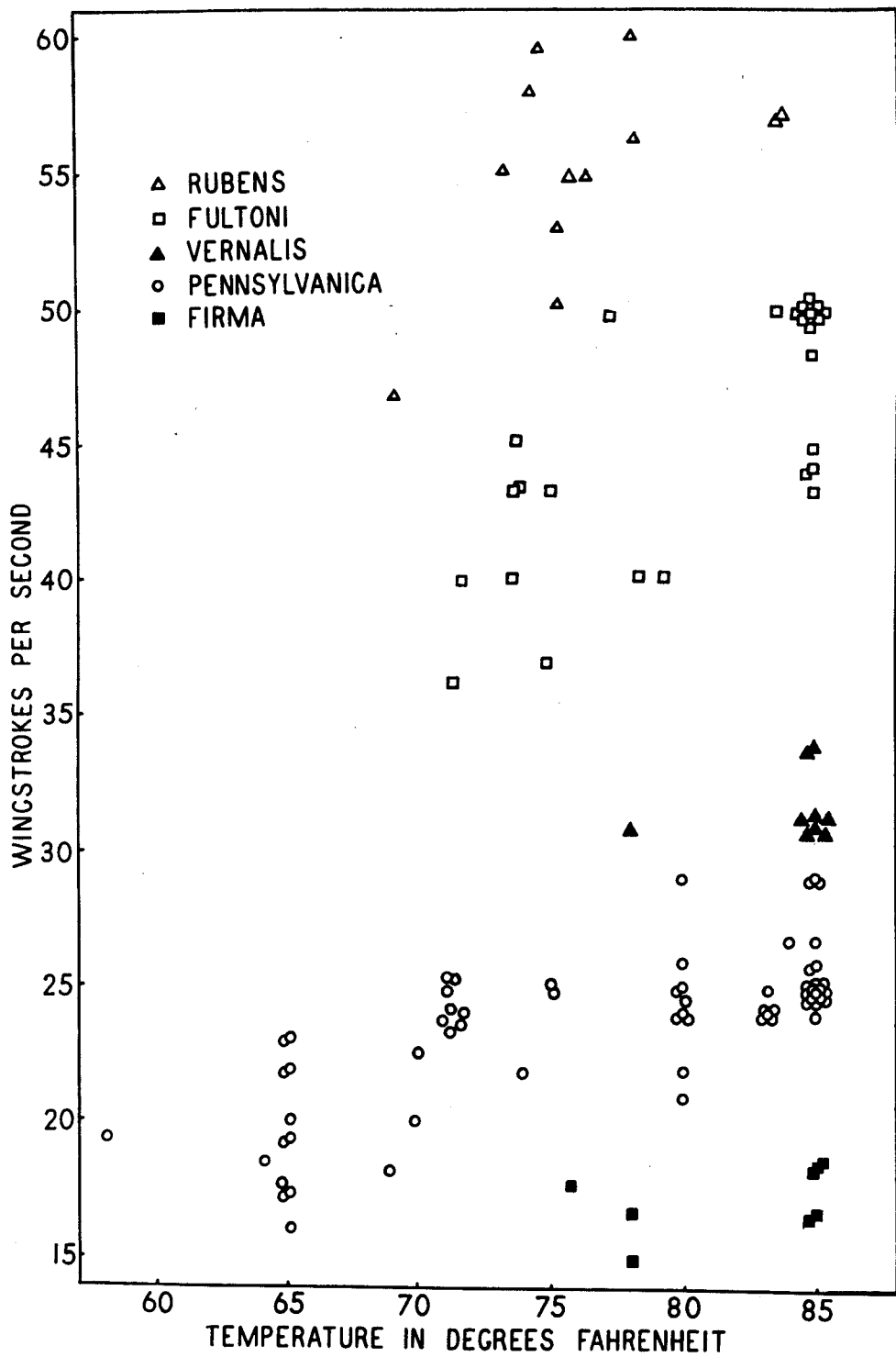


FIG. 15. The effect of temperature on rate of wing-stroke in the calling songs of eastern field crickets.

still alive on September 30. Offspring from this mating appeared on September 30.

SONG RELATIONSHIPS

Geographic variation in the songs of field crickets was first noted by Allard (1910). Fulton (1952) first used it as a taxonomic character in this group. In the singing Gryllidae, Tettigoniidae, and Cicadidae, song differences have been responsible for the initial recognition of many undescribed species (Davis, 1922; Fulton, 1930; Pringle, 1955; Thomas and Alexander, 1957). As remarked by Dr. Edward S. Thomas in conversation with the writer, to one who has studied these groups in the field it is almost a foregone conclusion that two insects which occur in the same area and have different songs are different species.

As with most singing Tettigoniidae and Gryl-

crickets from the localities indicated in Figure 7. The recordings were made both in the laboratory and in the field, using a Magnecorder PT6A in the laboratory, and a Magnemite 610-E in the field. American Microphone Company D-33 and D-33A microphones were used in both cases, with a 24-inch parabolic reflector sometimes employed in the field. The audiospectrographs were made with a Vibralyzer (Kay Electric Company, Pinebrook, New Jersey). For further explanations of the use of this instrument and its portrayal of cricket sounds, see Borror and Reese (1952) and Alexander (1957).

Figures 9-14 show sample audiospectrographs from typical calling songs of each of the five field cricket species under consideration, and of the house cricket, *Acheta domesticus* (Linnaeus), a species introduced from Europe. The house cricket recording was made of an individual from

TABLE I
COMPARISON OF SONG CHARACTERISTICS IN EASTERN FIELD CRICKETS

Species		<i>firma</i>	<i>pennsylvanica</i>	<i>vernalis</i>	<i>fultoni</i>	<i>rubens</i>
Number of Individuals Recorded		11	74	11	37	12
Pulses/Second (85° F.)	Range	17-19	24-29	30-33	43-50	60
	Mean	18	25	31	49	60
Chirps/Minute (85° F.)	Range	56-168	120-370	108-246	176-420	—
	Usual Number	100-120	150-240	180-200	300-360	—
Pulses per Chirp	Range	4-6	3-7	2-4	2-4	—
	Mode	4	4	3	3	—
Degree of Dominance of Pure Frequency	Rank from most "musical" to least "musical"	1	1	3	3	2
Intensity	Rank from loud- est to softest	2	1	4	4	3
Frequency (Toothstrike Rate)	Rank from high- est to lowest	5	4	2	3	1

lidae, male field crickets ordinarily space themselves in the field and remain in one spot all their adult lives. A large part of the time they produce a sound which is generally referred to as the calling song (also solitary or common song). This is the only sound which will be discussed here. The variety of sounds made by field crickets in other situations is discussed by Alexander (1957). The calling song attracts the adult females which move toward and locate the males. The roving females are seen much more often in the field than the sedentary males, and dominate collections for this reason.

Tape recordings and audiospectrographs have been made of the calling songs of 145 field

a culture supplied to Ohio State University from the University of Missouri.

A number of analyzable characters appear in *Acheta* sounds, such as the frequency (rate of toothstrike) (individual toothstrikes are not shown in Figures 9-14), rate of pulsation (wingstroke rate), rate of chirping, regularity of chirping, number of pulses per chirp, and "musical" quality or degree of dominance of the pure frequency. Figure 15 is a scatterdiagram comparing the songs of all individuals recorded at known temperatures with respect to what is probably the most significant character, rate of wingstroke, or rate of production of sound pulses. Both laboratory and field recordings are

included, and much of the infraspecific variation is probably due to error in measuring temperatures. Table I is a comparison of several characteristics of the calling songs of eastern field crickets.

All of the eastern field crickets sing both day and night, though *vernalis*, *fulloni*, and *rubens* do most of their singing at night. The songs of these three crickets are soft and somewhat less musical when compared to the loud, clear chirps of *pennsylvanica* and *firma*. *A. vernalis* and

fulloni chirp more rapidly and more regularly than do *pennsylvanica* and *firma*, with *vernalis* being somewhat intermediate between the two extremes in this respect. Differences in qualities such as these are difficult to describe adequately, though they may actually be recognition characters for an observer distinguishing the songs of the different species. For example, *fulloni* chirps with considerably more regularity in southern Ohio than it does across the Appalachians in Virginia and North Carolina. This difference

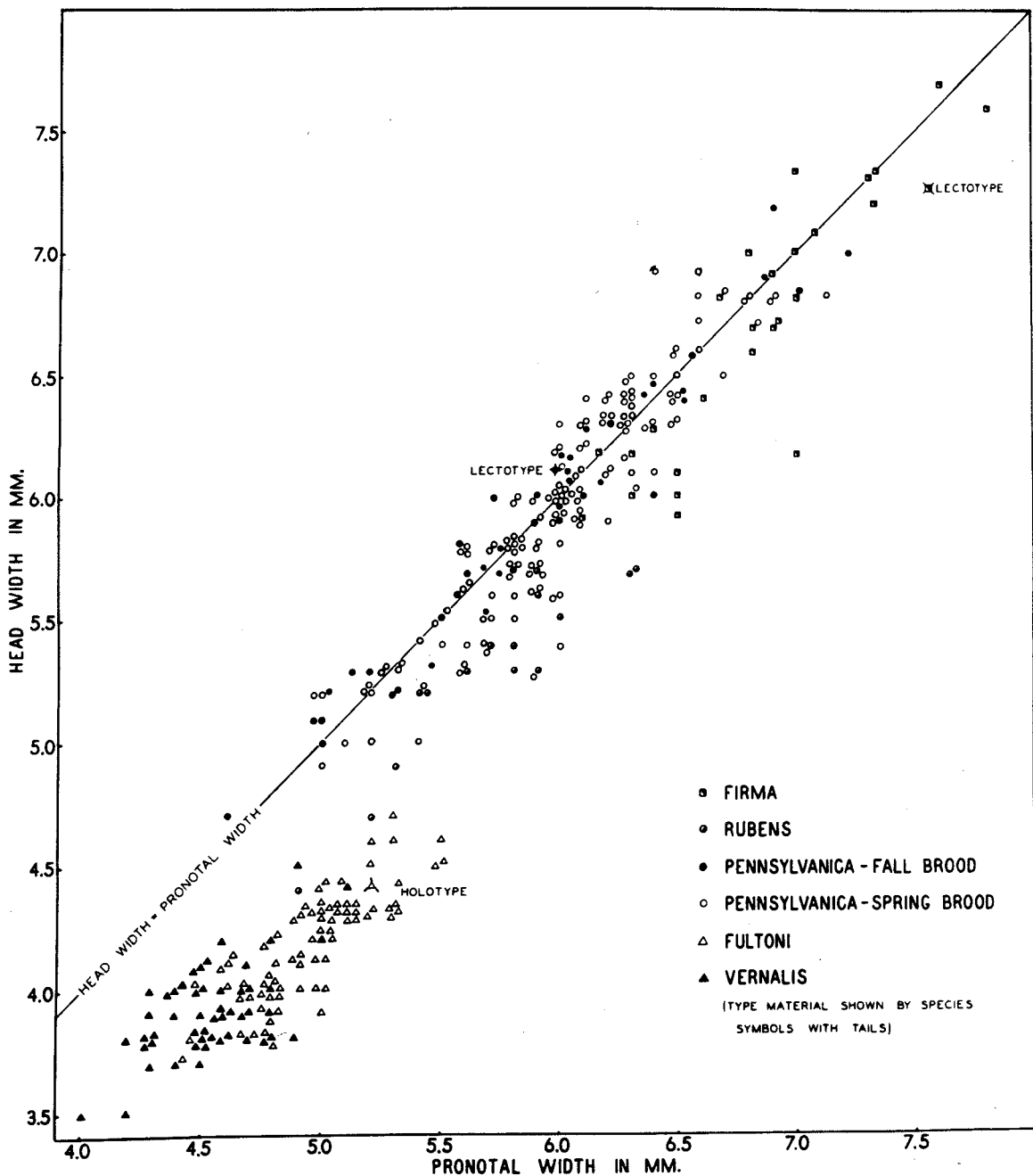


FIG. 16. The relative widths of head and pronotum in eastern field cricket males.

seems to be associated with the variation in ecology already mentioned. If uniform or rhythmical intervals in these songs are behaviorally significant, this introduction of an additional and different rhythmical element into the song of *fulltoni* may be associated with its occurrence together with *pennsylvanica*, an irregular chirper. In the south, *fulltoni* ordinarily occurs together with only one other species, *rubens*, which has a trilling song.

The chirping rate is not always the same in a single individual. One unmated male of *pennsylvanica* was timed singing at 120 chirps per minute shortly after molting to adulthood, and

three weeks later the same male, still unmated and still caged alone, was timed singing steadily at a rate of 370 chirps per minute.

Although in certain cases other characters are more 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 thus far. The recorded calling songs of all species can be separated by audiospectrographic analysis with 100 percent accuracy. Not enough courtship songs have been recorded to make comparisons, but it appears that these are more variable and less distinctive than the calling songs.

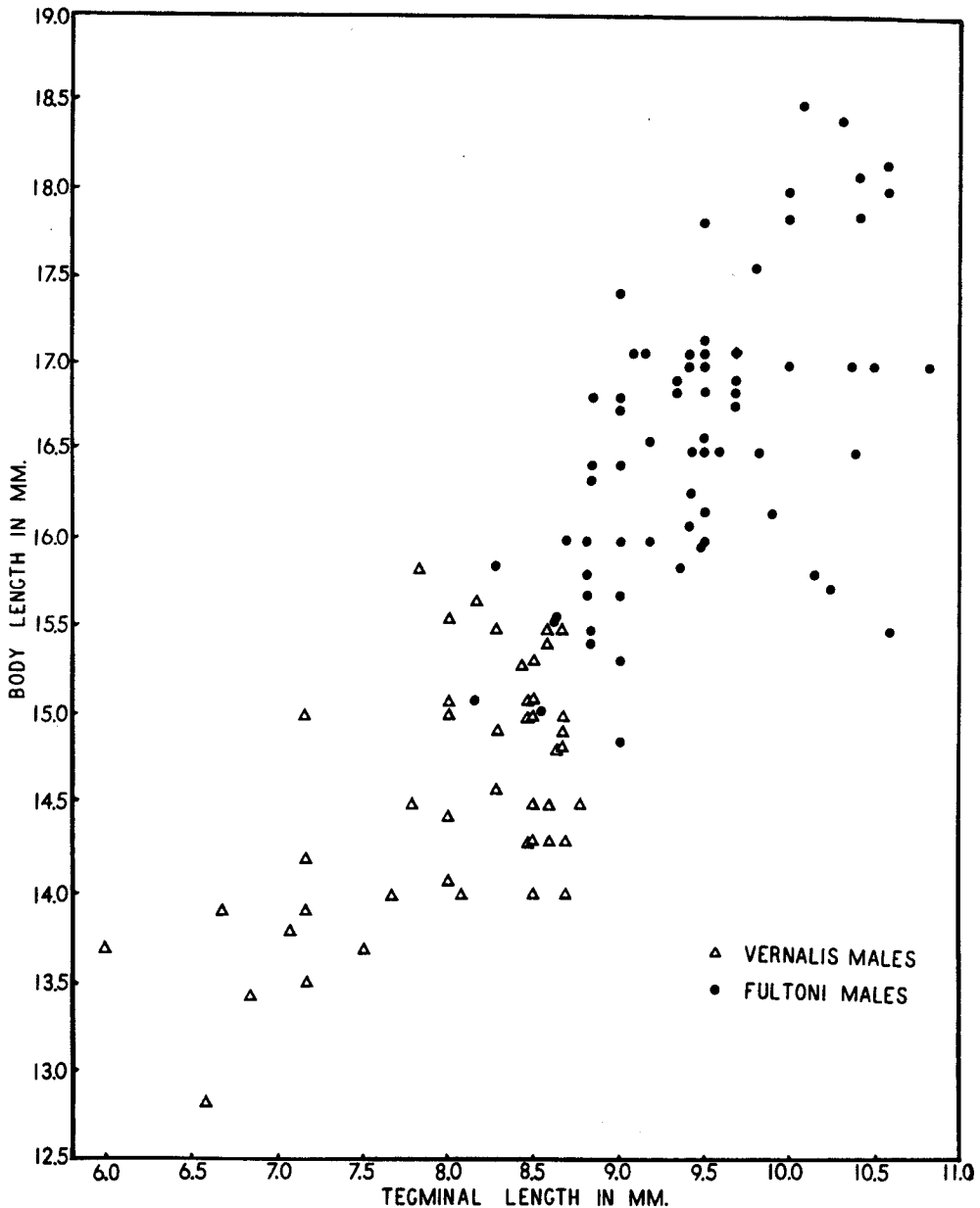


FIG. 17. The relative lengths of body and tegmina in males of *Acheta vernalis* (Blatchley) and *A. fulltoni* n. sp.

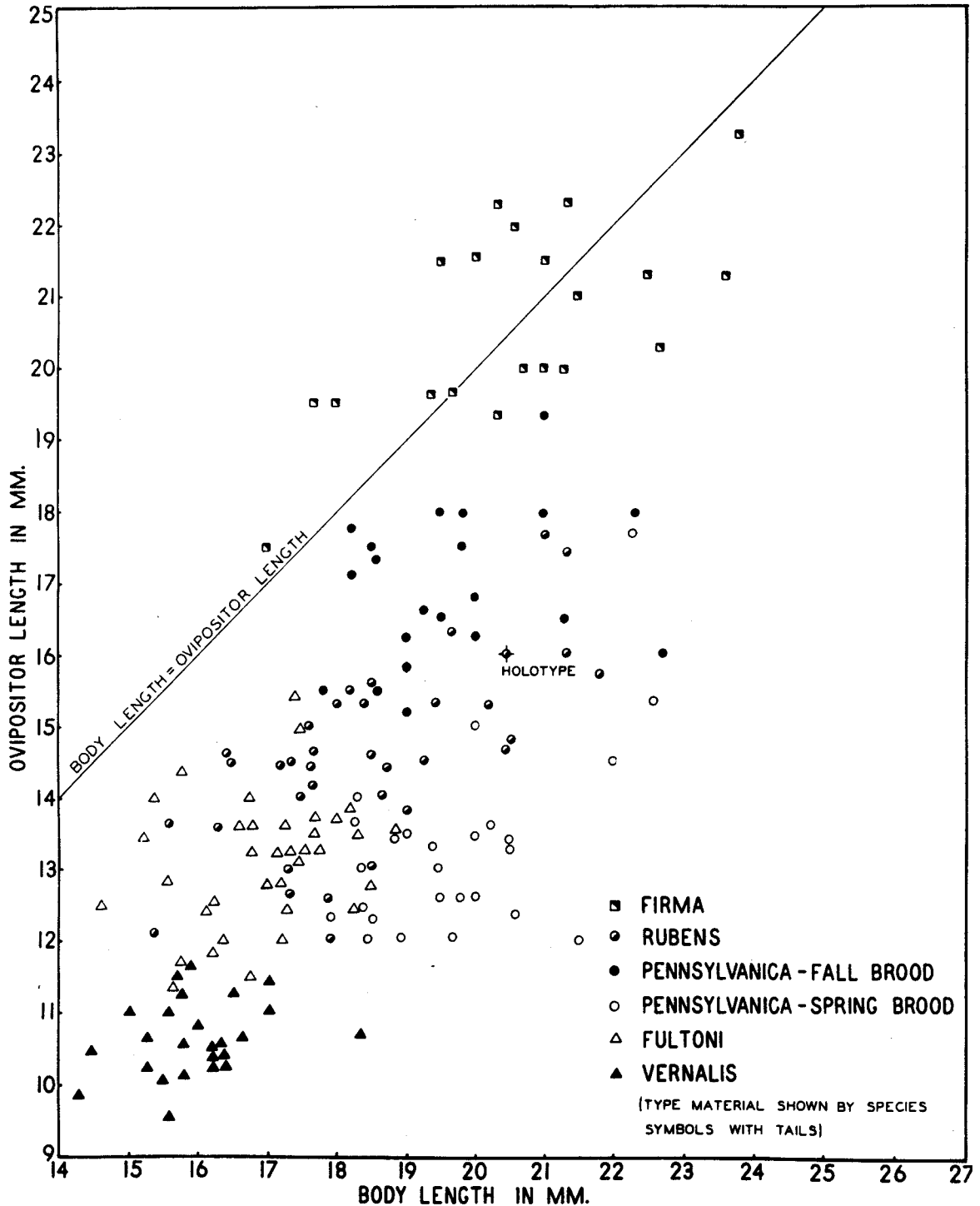


FIG. 18. The relative lengths of body and ovipositor in females of eastern field crickets.

MORPHOLOGICAL CHARACTERISTICS

The morphological characters found to be of value in this study were body proportions, size, coloration, and the 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 morphological character was found which would separate all five species. Except for *vernalis*, both sexes of which are distinguishable from all the other species, most pairs of species can be distinguished in one sex only. The scatterdiagrams comparing morphological characters (figs. 16-18) are based almost entirely on the writer's collection, with type material located as designated.

Dimorphism in the length of the hind wings is exhibited by *pennsylvanica*, *firma*, and *rubens*, while only short-winged individuals of *vernalis* and *fulloni* have been collected in the field. Some individuals of *fulloni* reared on a high-protein dog food diet and under crowded conditions developed underwings slightly longer than the tegmina, but similar conditions never produced long-winged *vernalis*. Almost 100 percent of the individuals of *pennsylvanica* and *rubens* reared under these conditions develop long wings. Some authors have considered this character to be of no value since it was discovered that long-winged parents may produce short-winged offspring and short-winged parents may produce long-winged offspring. However, the ability to develop underwings functional in flight has apparently been completely lost in *vernalis* and *fulloni*.

As shown in figure 16, all species except *pennsylvanica* and *firma* have the head invariably narrower than the pronotum. In such species, the pronotum is generally widest near its posterior margin and the head appears somewhat retracted (figs. 5, 6). In *pennsylvanica* and *firma*, especially the males, the reverse is true, with the widest part of the pronotum near its anterior border, and the head as often wider than the pronotum as not, and rounded or swollen in appearance (figs. 1-3). This character of proportionate width and general conformation of the head and pronotum readily separates the males of *fulloni* and *vernalis* from those of the other species.

With respect to coloration, *vernalis* represents an extreme, being nearly always totally black. A few specimens have small reddish areas near the base of the hind femora. *A. pennsylvanica* varies from totally black specimens to specimens with light brown tegmina, pale or reddish hind femora, and pale or reddish spots on the sides of the pronotum. The pale forms are most commonly encountered in sandy areas, such as around

the Great Lakes. In the writer's collection, only one out of 280 specimens of *pennsylvanica* has reddish spots on the sides of the pronotum, while 33 out of 54 specimens of *rubens* do. At present this is the best morphological character known for separating these two species. Since the ranges of these two species overlap rather narrowly, a high proportion of specimens can be separated on the basis of distribution and the coloration of the pronotum.

A. rubens and *firma* are similarly marked, generally having brown tegmina and pale or reddish hind femora, in addition to generally having reddish patterning on the sides of the pronotum. *A. fulloni* also has brown tegmina and at least partially reddish hind femora. It is separable from *vernalis* in both sexes on the basis of color alone.

A. vernalis is the smallest of the five species, with the smallest specimens seen only 12.8 mm. in body length (male). *A. firma* is the largest, with specimens in the writer's collection up to 24 mm. in body length (female). This is probably not a good indication of the upper limit in size for *firma*, but specimens positively identified as *firma* in this study are limited to those for which data other than morphological characteristics are available. Fulton (1952) includes a small number of beach crickets in the class with a body length of 26-29 mm., and Rehn and Hebard (1915) list the range of body length for American *Acheta* as from 14.0 mm. to 28.8 mm. *A. fulloni* averages slightly larger than *vernalis*, with considerable overlap, and *pennsylvanica* and *rubens* average smaller than *firma* with considerable overlap. *A. rubens* averages slightly smaller than *pennsylvanica*, and individuals from the fall brood of *pennsylvanica* average a little smaller than those from the spring brood.

As shown in figure 18, the females of *firma* are separable from those of all the other species on the basis of relative lengths of the ovipositor and body. The fall and spring broods of *pennsylvanica* are also partially separable on this basis, and the location of the syntypes of *pennsylvanica* on this diagram indicates that these were fall specimens, which is to be expected since the fall brood is generally present in larger numbers and is better represented in collections.

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 male collected in a field in southern Ohio in which both *fulloni* and *pennsylvanica* occur. This specimen, though having the narrow head and general body proportions of *fulloni*, had long black tegmina and fully developed underwings, and was larger than any *fulloni* collected. Its chirping had the typical regularity and speed of wing motion of *fulloni*, but the chirps

were four-pulse and delivered at a regular rate of about 240 per minute (80° F.). It failed to produce offspring when mated with a *pennsylvanica* female from the spring brood.

Figure 19 is a composite diagram showing the 50 crosses and 25 controls completed by Fulton (1952) and 30 additional crosses and 34 controls completed in the present study. The three successful crosses probably do not reflect a lack of reproductive isolation in the field. Adults of

has been heard or collected in the field. It seems likely that song differences are of importance in this regard, although tests have not yet been performed 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

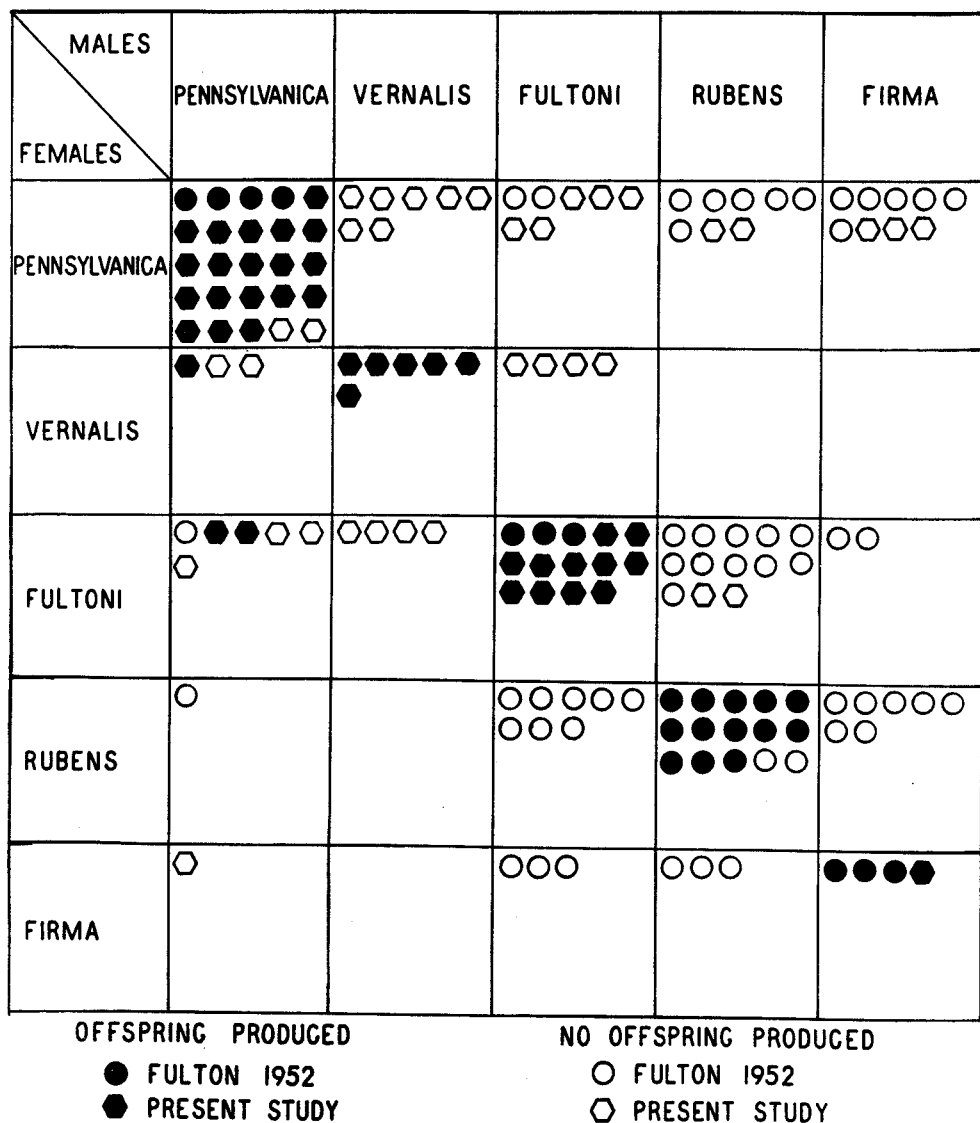


FIG. 19. Crossing experiments with eastern field crickets.

fultoni and *pennsylvanica* 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 suggestion is strengthened by the fact that only one presumed hybrid

matings. It was noted that in matings set up at the same time these events took place sooner in the controls than in the crosses. Males in cross-matings were heard singing the calling song much more than those in the 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 to the songs of males of their own species coming from other cages in the room, or simply to a change in the physiological condition of unmated females.

PHYLOGENETIC IMPLICATIONS

Our knowledge of the distributional and other relationships of the *Acheta* species is too scanty to allow any great amount of speculation as to their origin. However, certain historical aspects seem worthy of mention.

Three of the crickets under consideration have the ability to produce long-winged individuals (*pennsylvanica*, *rubens*, *firma*), one does not (*vernalis*), and one does so only rarely and probably imperfectly (*fulloni*). Wing reduction here is probably a secondary condition, the short-winged forms being derived from a population with the ability to form long wings. As pointed out to the writer by Dr. Fulton, in this genus as well as 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. The exact stimulus for expression of this potentiality is unknown, though it may be connected with crowding or with diet. High proportions of long-winged individuals of *pennsylvanica* and *rubens* are formed in the laboratory in crowded cultures reared on high-protein dog food. At any rate, a high degree of correlation between the capacity to produce individuals capable of flight and the degree of instability or lack of permanence in the habitat would appear to have obvious advantages.

A. pennsylvanica and *rubens* have both spring and fall broods, though these may differ somewhat in their relations to each other. Of the other species, *fulloni* and *vernalis* are spring crickets, and *firma* is a fall cricket. Both *pennsylvanica* and *rubens* exhibit considerable variation in most characters studied, while *fulloni* and *vernalis*, especially, are quite uniform.

From all these comparisons one might speculate that the common ancestor of all these species was a double-brooded cricket which probably occurred in some sort of unstable or impermanent habitat and possessed the ability to produce long-winged individuals.

Settlement and clearing have undoubtedly brought about drastic changes in the relative numbers and distribution of the field crickets in eastern United States. Prior to settlement, about 95 percent of the state of Ohio was forested and five percent was prairie. Today, only about five percent of the state is forested, and the rest is chiefly involved in agriculture and perpetually in various types of grassy, weedy, or cultivated

siuations. Today the range of *pennsylvanica* is fairly continuous across Ohio, Indiana, and Illinois, while *vernalis* and *fulloni* occur only in small isolated colonies. The uniformity of these last two species across a range of 300 to 400 miles from east to west suggests, however, that their distribution was once fairly continuous. It is probable that *vernalis* was once the most abundant field cricket in this area, and *fulloni* must have occurred more or less continuously across the southern half of these states.

One of the most important consequences of finally viewing the various populations of *Acheta* correctly as distinct species, is in the effect on our reconstruction of their distributional history. It is apparent that these species could not have developed as "local" adaptations to environmental conditions, with distributional relationships such as those prevailing today, and that geographic isolation on a grander scale must have once occurred. The general distributional relationships of the *Acheta* species illustrate patterns very similar to those occurring between other similarly related forms in the genera *Amblycorypha*, *Neoconocephalus*, *Pterophylla*, *Oecanthus*, and *Anaxipha* (unpublished data). It seems likely that similarly related forms, perhaps also poorly defined morphologically, may exist in the non-singing Orthoptera.

KEY TO SPECIES OF *Acheta* OCCURRING IN EASTERN UNITED STATES

As has already been indicated there are many cases in which preserved field crickets cannot be positively identified by morphological characters alone. One is tempted to write a key utilizing song characters, and geographical, ecological, and seasonal distribution, as well as structural features. However, these characteristics can be compared more easily by simply referring to the various illustrations. The following key is based chiefly on morphological characters, and will distinguish most preserved specimens. It should be remembered that deviations from the coloration described here may occur in specimens collected in molasses traps and cleaned by passing through various solutions, and in very old dried specimens. Thus, old pinned specimens of *vernalis* often develop a dull blackish red coloration, though newly pinned specimens retain the solid black color of living individuals.

1. General coloration straw or dull brownish-yellow; head and pronotum dark brown, mottled with paler areas; head with an irregular dark, transverse bar extending between the eyes near their dorsal border, narrower light bars in front of and behind this bar. . . . **domesticus**
- 1'. General coloration ranging from solid black to dark brown, tending toward reddish in paler specimens rather than toward straw-color; head and pronotum black, with or without pale markings; head without transverse bars. 2
- 2(1'). Pronotum of male widest near its posterior border; head of male definitely narrower than

pronotum, presenting a retracted appearance, not exceeding 4.7 mm. in width; body length 12.8-19 mm.; ovipositor length 9.5-15.5 mm.; always micropterous in both sexes. 3

2'. Pronotum of male usually widest near or anterior to its middle; head of male as often wider than pronotum as not, presenting a swollen globose appearance, almost always over 4.7 mm. in width; body length 15-29 mm. or more; ovipositor length 12-24 mm. or more; macropterous or micropterous in either sex. 4

3(2). Coloration solid black, rarely a dash of reddish on the inside or outside of base of hind femora. **vernalis**

3'. Tegmina always brown; hind femora usually reddish or pale, at least on basal third; tibiae pale. **fulloni**

4(2'). Found along the Atlantic Coast (and probably the Gulf Coast), and in sandy areas in the Southeast; body usually over 18 mm. in length; ovipositor 19-23 mm. or more in length and as often longer than the body as not. **firma**

4'. Found in fields and grassy areas throughout eastern United States, including the areas described above; body rarely over 23 mm. in length; ovipositor rarely over 18 mm. in length, and always shorter than body. 5

5(4'). Pronotum usually with reddish or light-colored spots on sides; southern crickets occurring northward only into the Appalachians and to the southern tips of Illinois and Missouri. **rubens**

5'. Pronotum almost always lacking light spots on sides, except in crickets collected in northern sandy areas, such as around the Great Lakes; northern crickets extending southward to just below the Appalachians. **pennsylvanica**

SUMMARY

The singing Tettigoniidae and Gryllidae of eastern United States contain a number of species which have not received formal recognition by taxonomists because morphological characters are not known by which preserved specimens can be distinguished. Among these are five species of *Acheta*, four of which were shown by Fulton (1952) to be non-interbreeding populations in North Carolina. All but one pair of these species can now be separated, in at least one sex, on the basis of morphological characters whose value had previously been obscured by (1) attempts to deal with the whole genus at once, and (2) studies based on morphological relationships alone. All five species can be separated on the basis of song differences revealed by audio-spectrographic analysis.

Acheta pennsylvanica (Burmeister) is the most abundant species in northeastern United States. It occurs in grassy and weedy areas, has a chirping song, and has two single-brooded populations, one adult in spring and one adult in fall. *A. rubens* (Scudder) is the most abundant species in southeastern United States. It also occurs in grassy and weedy areas, but it consists of a single, double-brooded population, producing both spring and fall adults, and it has a trilling song. *A. vernalis* (Blatchley) and *A. fulloni* n. sp. are chirping crickets which occur in leaf litter in

woods in northeastern and southeastern United States, respectively. *A. firma* (Scudder) is a chirping fall cricket which occurs along the Atlantic coast south from Delaware, and inland in sand hills in North Carolina. North-south variations in ecology and song occur in *A. fulloni*, and certain variations in life history occur in *A. pennsylvanica*.

It is probable that at least one eastern species and several western species of *Acheta* in the United State are as yet unrecognized.

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