

SYSTEMATIC AND BEHAVIORAL STUDIES ON THE CRICKETS
OF THE NEMOBIUS FASCIATUS GROUP (ORTHOPTERA:
GRYLLIDAE: NEMOBIINAE)¹

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ABSTRACT

The three eastern species in the *Nemobius fasciatus* group, generally treated by orthopterists as subspecies or races, can readily be separated as living individuals, and most pinned specimens can now be identified through the use of combinations of easily observed morphological characters. Extensive distribution records, chiefly compiled by listening for singing males, show that the three species have broadly overlapping ranges. Observations on local populations have revealed occasional instances where individuals of two, or all three, of the species are mixed together with no indication of interbreeding. *N. allardi*, n. sp., previously called *N. fasciatus fasciatus* (DeGeer), occurs chiefly in grassy and weedy areas in well-drained locations over most of northeastern United States and has a clear musical trill. *N. tinnulus* Fulton occurs in or near leaf litter in xeric woodland areas in central eastern United States, and its song is a slow trill in which the sound pulses are heard as individually distinct

units and can be counted by ear at low temperatures. *N. fasciatus* (DeGeer), previously called *N. fasciatus socius* Scudder, is less closely related to the other two species than they are to each other. It occurs in wet situations over nearly all of eastern North America, including Florida, with its northern limits somewhere in southern Canada, south of the limits of *N. allardi*. Its song consists of a series of buzzy chirps, and is quite distinct from the songs of the other two species and surprisingly like the songs of *Miogryllus* species. Audio-spectrographic analysis of tape recordings of the calling and courtship songs of the three species demonstrate relationships which correlate with morphological evidence. Comparison of the courtship behavior of the males of various Nemobiinae, Gryllinae, and other crickets shows that the sequence can be divided into three major segments, with homologies and analogies suggested in certain cases.

The crickets of the *Nemobius fasciatus* group are small, ground-inhabiting species occurring in North America from southern Canada to northern Mexico and east of the Great Basin in the United States. All of the crickets in this group were placed by Hebard (1913) in the species *Nemobius fasciatus* (DeGeer), which he considered to have three subspecies, *socius* Scudder and *abortivus* Caudell, in addition to the typical form. Fulton (1931) described a fourth subspecies, *tinnulus*. In spite of wide discussion of this interesting group by biologists all over the world subsequent to the excellent studies of Fulton (See Chopard 1938; Emerson 1945; Thorpe 1948; Mayr 1948; Pierce 1948; Richards 1952, 1953; Gabbutt 1954; and Hubbell 1954), the taxonomic status of the different morphological and song forms has remained somewhat obscure. Publications by orthopterists have continued to refer to them as subspecies or as physiological, ecological, or geographic races (See Fulton 1933, 1937; Hebard 1934, 1936, 1938, 1945; Cantrall 1943; Friauf 1953). In some cases any and all forms encountered have been designated simply as *Nemobius fasciatus* (DeGeer) (Strohecker 1937; Froeschner 1954). This treatment is apparently due to difficulty encountered in separating the different forms by morphological characters.

The results published by Fulton (1931, 1933, 1937) were sufficient to demonstrate clearly that the forms he called *fasciatus*, *socius*, and *tinnulus* are distinct species, whether or not one chooses to recognize them by formal nomenclature. This was pointed out by Emerson (1945), and also by Mayr (1948), who mentioned the observations of Cantrall (1943), but unfortunately referred to these ground crickets as "tree crickets" (pp. 227, 230). Hubbell (1954) is reluctant to honor such morphologically ill-defined forms with formal nomenclature. However, the continued misinterpretation of Fulton's findings, in spite of his statement, "I believe that the three subspecies are physiologically distinct and that any individual belongs to one of the three . . ." (1931, p. 213) makes it clear that to force proper recognition of the relationship of the forms and provoke the small amount of field work necessary to establish which ones should be included in local faunistic surveys and similar investigations, they must be referred to as distinct species nomenclaturally as well as otherwise. Froeschner (1954), for example, treats all forms under the single name, *fasciatus* (DeGeer), following Fulton's suggestion for "any general discussion where fine distinctions are not involved" (1931, p. 213). That this is not satisfactory is evidenced by Froeschner's statement (p. 316) that "although a number of categories less than a species have been recognized with a name (the woodland race *N. tinnulus* was described in part from Iowa by Fulton) many of these were simply color varia-

¹The part of this work involving detailed studies of the songs and singing behavior was carried out by Alexander, aided by a grant from the Rockefeller Foundation. The rest of the material is a joint contribution. Accepted for publication February 5, 1959.

tions or responses to differences in habitat." Analogous morphological variations may appear in a species in similar habitats which are isolated from each other, as in *Acheta pennsylvanicus* (Burmeister) (See Alexander 1957b) and probably do so in most or all species to one degree or another as a result of parallel selection. However, there seems to be no justification for ignoring song variations correlated with habitat or implying that these represent local adaptations to environmental conditions. Such misinterpretations result in a false conception of distributional history which in this group must have involved geographic isolation of the different forms, with macrogeographic sympatry occurring only after they had become reproductively isolated. The distinctness of the three eastern species is proved by their frequent co-existence in the same habitats without any indication of interbreeding.

NOMENCLATURE AND SYNONYMY

We have examined all of the existing types in this group, and as a result are forced to make the following nomenclatural changes.

Nemobius fasciatus (DeGeer)

The Striped Ground Cricket

Gryllus fasciatus DeGeer, 1773, p. 522, Pennsylvania; Naturhistoriska Riksmuseet, Stockholm, Sweden (a single, macropterous female with labels "170, 5F," "*Gryllus fasciatus* DeGeer") (See figs. 2, 3).

Acheta hospes Fabricius, 1775, p. 281, America; Universitetets Zoologiske Museum, Krystalgade, Copenhagen K, Denmark (a single, macropterous female with label, "hospes").

Acheta vittata Harris, 1841, p. 123, Massachusetts; type lost. There is no indication that Harris distinguished this species and *allardi* (new species described below). However, the only part of his description which applies to only one of the two species applies to *fasciatus*: "In the brownish-colored varieties three longitudinal black lines are distinctly visible on the top of the head . . ." Either this character or the "black line on each side of the thorax, which is continued along the sides of the wing-covers to their tips," appears to be the basis for Harris' name, *vittata*. The latter is characteristic of both *allardi* and *fasciatus*. On this basis, we believe that this name cannot be justifiably used for any species other than *fasciatus* (DeGeer). Prior to its being placed in synonymy by Hebard (1913), *vittata* was used by different authors for either one or both of these two species.

Nemobius socius Scudder, 1877, p. 57, Georgia; Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts (a single, micropterous female with the following labels: "Scudder's type 1876," "Geo.," "Type 14053," "*Nemobius socius* Scudd.," "Cab. S. H. Scudder.")

Nemobius tinnulus Fulton

The Tinkling Ground Cricket

Nemobius tinnulus Fulton, 1931, p. 210, Raleigh, North Carolina; U. S. National Museum (male holotype).

Nemobius allardi, new species

Allard's Ground Cricket

This is the species which has most often been called *fasciatus* in the past, erroneously as is

shown in figures 2 and 3. It is here named in honor of Dr. H. A. Allard, who had described the songs and ecology of all three of the eastern species discussed here as early as 1910. Although he did not refer to them as distinct species, he recognized that three forms existed and was the first to describe their biological differences accurately and in a clearly recognizable fashion.

Holotype Male: (In University of Michigan Museum of Zoology) Collected and song tape-recorded (In UMMZ tape library) by Richard D. Alexander on the Ohio State University Campus, Columbus, Ohio, 3 July 1954, in a mowed lawn. Micropterous; general coloration brown with darker markings; conformation of head and pronotum as shown in figure 2; dorsal head striping limited to two lateral dark spots between the eyes representing the anterior culmination of the lateral stripes, and a dark central stripe which almost completely fades out toward the back of the head; pronotum slightly narrower at anterior border, and bordered laterally with a yellowish stripe (not visible from above); pronotum as seen from above bordered with black stripes which are separated from the dark median portion by yellowish areas of irregular width; dorsal surface of abdomen black, ventral surface brown; appendages brown; tegmina light brown with a dark band on inner side of lateral field and dark spots along the median side of each tegmen and at base of stridulatory vein; underwings extending only to about the stridulatory vein on the tegmina; stridulatory vein on right tegmen 0.95 mm. in length from inner end to ulnar vein, 1.40 mm. in length from inner end to point at which vein becomes curved so that it is most nearly perpendicular to base of tegmen.

Allotype Female: (In UMMZ) Collected by Edward S. Thomas and John S. Thomas in Monroe Twp., Madison County, Ohio, 24 October 1933. General form and coloration same as in holotype, except coloration a little more reddish and tegmina shorter, exposing four abdominal tergites.

Measurements of Holotype and Allotype (in millimeters, made with an ocular micrometer in a binocular microscope): Body length, ♂, 9.15, ♀, 9.60; pronotal length, ♂, 1.65, ♀, 2.15; greatest pronotal width, ♂, 2.50, ♀, 2.94; head width behind eyes, ♂, 2.20, ♀, 2.65; length of right hind femur, ♂, 5.80, ♀, 6.95; length of right tegmen, ♂, 5.25, ♀, 3.40; length of ovipositor, 7.9.

Paratypes: (In Ohio State Museum) 7 micropterous ♂♂, 12 micropterous ♀♀; Madison Co., O., Monroe Twp., 24 Oct. 1933, E. S. and J. S. Thomas; micropterous ♂ and ♀, Mercer Co., O., Mendon Twp., 2 Sept. 1932, T. H. Hubbell; micropterous ♂, Franklin Co., O., Columbus, 29 Sept. 1932, E. S. Thomas; micropterous ♀, Lucas Co., O., Little Cedar Point, 23 Aug. 1932, E. S. Thomas and L. W. Campbell; micropterous ♀, Geauga Co., O., Bainbridge

Twp., 21 Aug. 1937; micropterous ♀, Knox Co., O., Jefferson Twp., Sect. 1, 30 Sept. 1949, E. S. Thomas; micropterous ♀, Summit Co., O., Ira, James S. Hine; micropterous ♂ and ♀, Wood Co., O., Liberty Twp., 23 Oct. 1931, E. S. Thomas; macropterous ♂, Lake Co., Ind., Crown Point, 15 Aug. 1939, C. L. Gibson; macropterous ♀, Columbus, Ohio, 15 Aug. 1939, H. Mayer: (In U. S. National Museum) micropterous ♂ and ♀, macropterous ♂, 23 Aug. 1943, and macropterous ♀, 18 Aug. 1946, Giles Co., Va., Mt. Lake Biol. Sta., T. H. Hubbell: (In Illinois Natural History Survey Collection) macropterous ♂, Antioch, Ill., 25 Aug. 1925, T. H. Frison; macropterous ♀, Kankakee, Ill., 15 Aug. 1932, Ross and Mohr; micropterous ♂, Chicago, Ill., 22 Oct. 1903; micropterous ♀, Shawneetown, Ill., 12 Oct. 1932, Frison and Ross: (In UMMZ) macropterous ♂ and ♀ (latter, fig. 2), Champaign, Ill., 26 Aug. 1918, T. H. Hubbell; macropterous ♂, Livingston Co., Mich., E. S. George Reserve, 29 Aug. 1937, J. S. Rogers; macropterous ♂, Ann Arbor, Mich., 26 July 1921, R. F. Hussey; macropterous ♀, Livingston Co., Mich., E. S. George Reserve, 1 Sept. 1936, I. J. Cantrall; macropterous ♀, Washtenaw Co., Mich., Scio Twp., Aug. 1933, T. H. Hubbell; macropterous ♂, Iosco Co., Mich., Oscoda, 6-8 Aug. 1937, Hubbell-Cantrall; micropterous ♂, Livingston Co., Mich., E. S.

George Reserve, 30 Aug. 1932, P. F. Hickey; micropterous ♀, Livingston Co., Mich., Brighton Twp., 5 Sept. 1921, T. H. Hubbell; micropterous ♀, Johnson City, N. Y., Aug. 1924, A. J. Ellsworth (fig. 2); 10 micropterous ♂♂ and 10 micropterous ♀♀, Giles Co., Va., Mt. Lake Biol. Sta., 23 Aug. 1945, T. H. Hubbell.

This species is sibling to *Nemobius tinnulus* Fulton, from which it differs in song, in the occasional production of macropterous individuals, in coloration, in conformation of the head and pronotum, and in various other characteristics discussed elsewhere in this paper.

Prior nomenclatural misconceptions in this group were apparently due to failure to examine types located in Europe and to the erroneous idea that *fasciatus* (DeGeer) (called "*socius* Scudder") was a southern geographic race extending north only to the vicinity of the Fall Line (Hebard 1913, p. 424; 1934, p. 249). If this were true it would preclude application of the name, *fasciatus* (DeGeer), based on a specimen from Pennsylvania. However, as shown in figure 1, none of the species in this group is limited to a distribution anything like that supposed by Hebard. Hebard's description of the morphological relationships among the forms discussed by him, and examination by us of specimens determined by him as late as 1932,

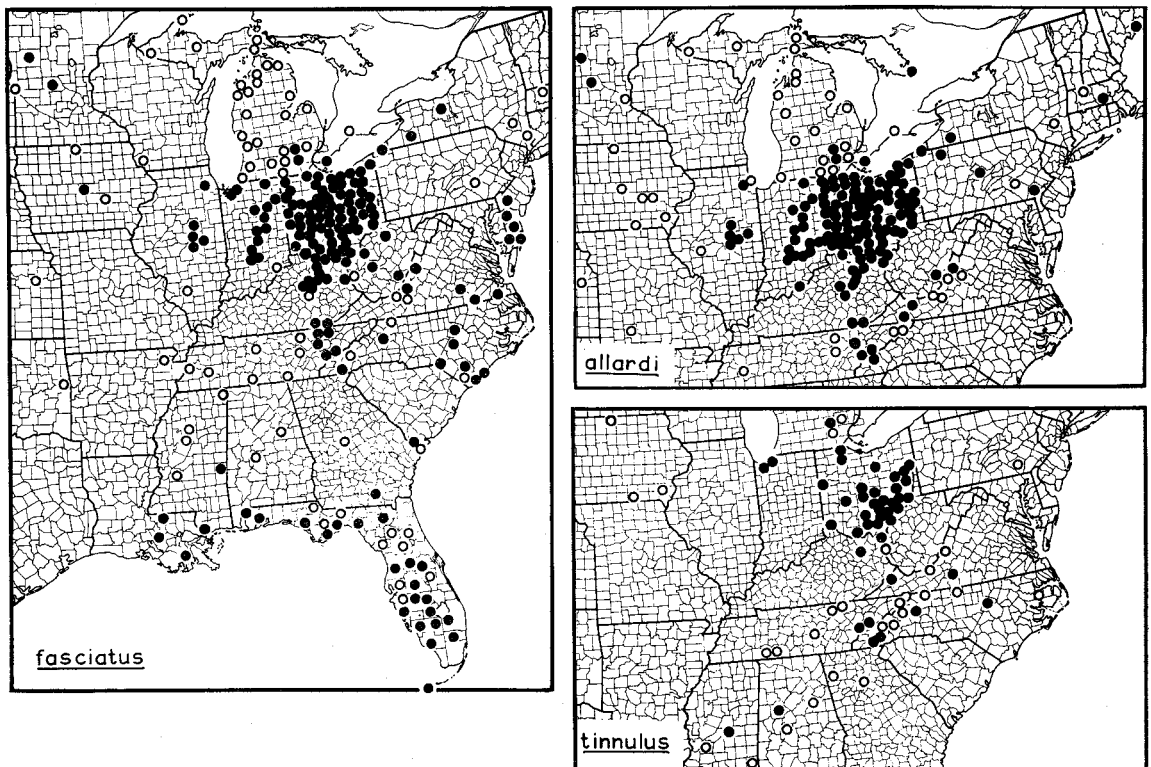


FIG. 1.—The geographical distribution in eastern United States of species in the *Nemobius fasciatus* group. Song records (both tape recordings and listening records) are indicated by closed circles, records based on specimens by open circles.

show that he included both *fasciatus* and *allardi* in his discussion of *allardi* (which he called "*fasciatus fasciatus*") and also in his discussion of *fasciatus* (which he called "*fasciatus socius*"). This seems to have been true of nearly every author who recognized that more than one form existed, with Fulton (1931, 1932, 1933, 1937), Cantrall (1943), and Pierce (1948) the only investigators who clearly recognized which species they were discussing at any particular time. Unfortunately, Fulton accepted the nomenclature of Hebard (1913) and assumed that his own ideas concerning the application of the names were the same as Hebard's. Thus, the names listed in the above synonymy have never been used in a clear-cut manner. This confusion is demonstrated by the following lists of the names which have been associated with the only recognizable descriptions of the songs of the three species under consideration here:

Nemobius fasciatus (DeGeer)

1. Scudder 1868, p. 3; *vittatus* (Harris)
2. Allard 1910a, p. 354; *fasciatus vittatus* (Harris)
3. Fulton 1931, p. 223; *fasciatus socius* Scudder
4. Cantrall 1943, p. 163; *fasciatus socius* Scudder
5. Pierce 1948, p. 129; *fasciatus socius* Scudder
6. Alexander and Borror 1956; *fasciatus socius* Scudder

Nemobius allardi, n. sp.

1. Allard 1910, p. 354; *fasciatus vittatus* (Harris)
2. Fulton 1931, p. 221; *fasciatus fasciatus* (DeGeer)
3. Cantrall 1943, p. 161; *fasciatus fasciatus* (DeGeer)
4. Pielmeier 1946, p. 338; *fasciatus fasciatus* (DeGeer)
5. Pierce 1948, p. 126; *fasciatus fasciatus* (DeGeer)
6. Alexander and Borror 1956; *fasciatus fasciatus* (DeGeer)

Nemobius tinnulus Fulton

1. Allard 1910, p. 41; *canus* Scudder
2. Fulton 1931, p. 222; *fasciatus tinnulus* Fulton
3. Cantrall 1943, p. 164; *fasciatus tinnulus* Fulton
4. Pierce 1948, p. 129; *fasciatus tinnulus* Fulton
5. Alexander and Borror 1956; *fasciatus tinnulus* Fulton

DISTRIBUTIONAL RELATIONSHIPS

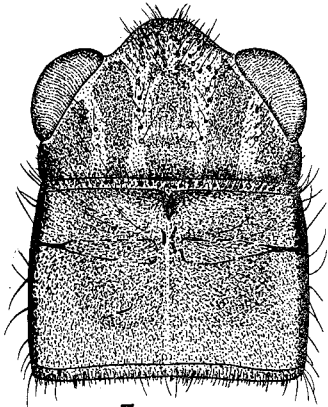
The known distribution of the three species under consideration here is shown in figure 1. Probably all three species extend farther west than is shown, but the scope of this paper has been limited to the areas in which we have been able to study the species in question in the field. With the exception of Fulton's Iowa work, we have excluded most material from west of the Mississippi River. We have seen specimens from every state bordering the Mississippi River on the west, and from as far west as Utah and Colorado. However, variations in coloration and body conformation, and in the length of the female ovipositor and the male stridulatory vein suggest that from one to three additional species may occur in this area. One of these (probably *canus* Scudder) extends from Colorado, Utah, and Texas eastward into Mississippi, Alabama, Georgia, western Tennessee, southern Illinois, and perhaps to the Atlantic Coast in South Carolina. Another (probably *abortivus* Caudell)

is largely northwestern, extending eastward and southward into North Dakota and Michigan. We have examined the types of both of these forms. *N. abortivus* Caudell is a small, dark cricket with a short ovipositor, but otherwise resembling *allardi*. The species which probably should be called *canus* Scudder is the largest in this group. In body conformation the cotypes from Dallas, Texas, resemble *fasciatus*, but they are generally more reddish in color, and the ovipositor and the stridulatory vein are usually longer than in *fasciatus*. One male examined (Dallas, Texas, not a cotype) had 160 teeth on the stridulatory vein, a figure intermediate between that obtained for *fasciatus* (100-145) and *allardi* and *tinnulus* (165-239) in eastern United States.

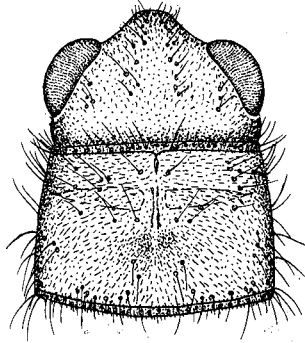
We believe that the possibility is extremely remote that any group such as this one can be correctly analyzed from pinned material, and therefore defer further remarks on western forms until field work with living material can be accomplished.

Because of difficulty in separating pinned specimens, records based on specimens alone have been considered generally less reliable than song records (either listening records or taped records), and are indicated in figure 1 as open circles. The State of Ohio is probably the only area which has been more or less thoroughly covered in terms of county distribution. This area has been worked intensively by Thomas during the past 25 years, and by Alexander from 1954 to 1958. Thomas has heard each species in every Ohio locality listed, and Alexander has duplicated about one-third of the Ohio records. Outside the State of Ohio most of the song listening records have been compiled by Alexander, with records by Thomas appearing in Ontario, Minnesota, Indiana, Pennsylvania, New York, Kentucky, Tennessee, and North Carolina. Recognizable song descriptions from definite localities have also been utilized from Allard (1910, 1910a), Fulton (1931), Cantrall (1943), and Pielmeier (1946). Records based on specimens alone have been compiled from the collections of the University of Michigan Museum of Zoology, the Ohio State Museum, and the Illinois Natural History Survey.

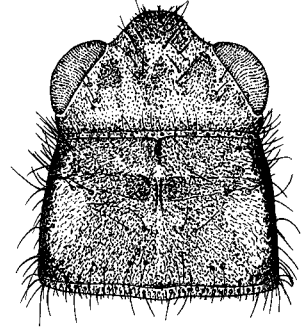
All three species have wider ranges than has been previously supposed. *Tinnulus* is limited to the areas which contain oak-hickory, oak-hickory-chestnut, or oak-pine woods, and it has a distribution similar to the combined ranges of the eastern wood crickets, *Acheta fultoni* Alexander and *A. vernalis* (Blatchley) (see Alexander 1957b). *Fasciatus* and *allardi* range over most of the eastern United States, though *allardi* is limited to the area of the Appalachian Mountains and northward, and *fasciatus* apparently does not reach as far north into Canada as *allardi*. It is likely that an obligate diapause limits the southern



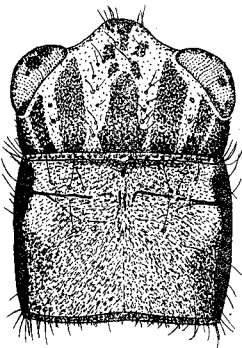
mic. ♂ - fasciatus
Illinois - 0.85 mm.



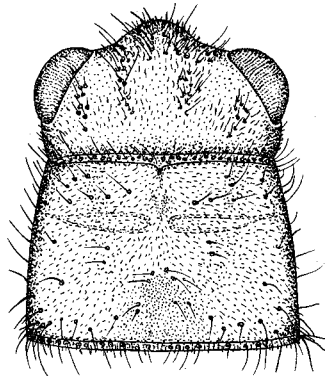
mic. ♂ - tinnulus
Illinois - 1.03 mm.



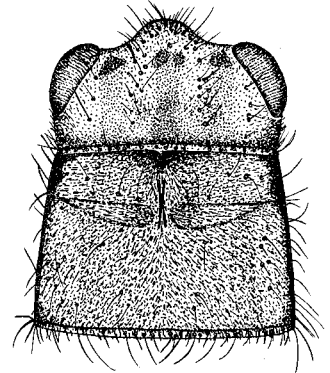
mic. ♂ - allardi
Ohio - 0.95 mm - Type



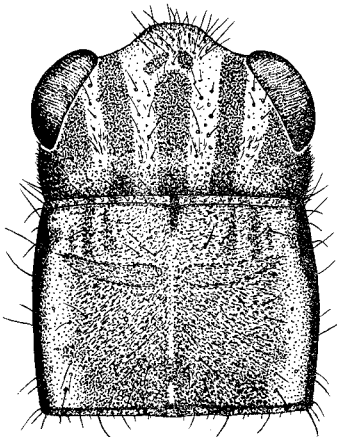
mic. ♀ - fasciatus
Mass. - 5.95 mm.



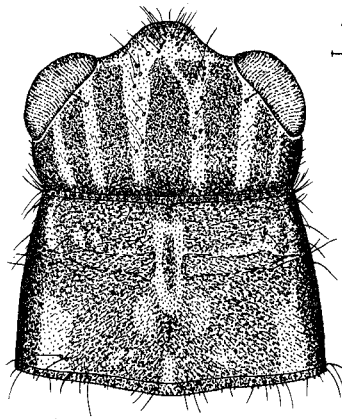
mic. ♀ - tinnulus
Illinois - 9.90 mm.



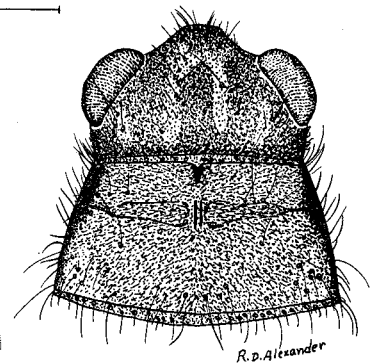
mic. ♀ - allardi
N. Y. - 8.20 mm



mic. ♀ - fasciatus
Florida - 7.55 mm.



mac. ♀ - fasciatus
Penn. - 8.55 mm - Type



mac. ♀ - allardi
Illinois - 7.5 mm.

1 mm.

R. D. Alexander

FIG. 2.—Typical conformations and patterning of the head and pronotum in macropterous and micropterous specimens of species in the *Nemobius fasciatus* group. For females, the measurements indicate length of ovipositor; for males, length of the stridulatory vein on the right tegmen as viewed from above.

distribution of *allardi*, as is apparently the case with *Acheta pennsylvanicus* (Burmeister), a species which has a very similar geographic distribution and occurs in the same habitat.

ECOLOGICAL RELATIONSHIPS

Our observations on the ecological relationships of the three species, made chiefly in Ohio, Indiana, and Illinois, correspond closely to the information given by Fulton (1931) and Cantrall (1943), for North Carolina and Iowa, and for Michigan, respectively.

Allardi is an inhabitant of grassy and weedy areas, such as lawns, pastures, fields, and roadsides, and is generally more abundant on slopes and in well-drained locations. *Fasciatus* characteristically occurs in marshes and in other low, poorly drained, grassy situations such as along stream banks and in bottomland pastures. *Tinnulus* is restricted to xeric woodlands and woodland borders, nearly always in leaf litter or pine needles in sunny or lightly-shaded oak-hickory, oak-hickory-chestnut, or oak-pine woods.

In hilly country within the range of *tinnulus*, all three species are often found in the same valley within a radius of a few hundred feet: *tinnulus* occupying the xeric southerly and westerly exposures; *allardi* occupying well-drained mesic situations, such as north- and east-facing slopes or the lower portions of drier slopes; and *fasciatus* occupying swampy places, usually in the bottoms of the valleys. *Allardi* and *tinnulus* are often found in colonies within a few yards of each other, as reported by Cantrall (1943), though they do not often come into contact. *Fasciatus* and *allardi*, however, sometimes intermingle at borderlines between mesic and hydric situations such as the periphery of low spots in pastures. Rarely, these two species have been found mixed together in colonies of considerable density in artificial situations, such as well-watered lawns.

On one occasion only, in September, Alexander found all three species completely mixed together in comparable proportions, in Hocking County, Ohio. The situation was a grassy, mowed clearing in a rather low area along a small stream. Leaf litter from the surrounding forest was scattered across the clearing. *N. maculatus* Blatchley, an inhabitant of leaf litter in woods, and *N. carolinus* Scudder, an inhabitant of moist, poorly drained situations, were also present in the clearing in small numbers.

To illustrate the combinations in which collectors may take these three species in series obtained from small areas, we analyzed a collection of 254 adults taken by T. H. Hubbell in 38 different localities in Giles County, Virginia, between July 23 and August 27, 1945, and 1946. Because Dr. Hubbell kept a log book in which he noted habitat and song, it was possible for us positively to identify practically every specimen.

This collection included 40 specimens of *fasciatus*, 154 of *allardi*, and 160 of *tinnulus*. *Fasciatus* was taken at 8 different localities, *allardi* at 28, and *tinnulus* at 22. Eleven collections were of a single specimen only. In the other 27 collections, each containing from 2 to 30 specimens, *fasciatus* was taken alone only 1 out of 7 times, *allardi* 9 out of 23 times, and *tinnulus* 2 out of 15 times. *Fasciatus* and *allardi* were taken together 4 times, *allardi* and *tinnulus* 13 times, and all three species were taken in the same series twice. Much of Dr. Hubbell's collecting was done along forest borders and in small clearings, and it is likely that he frequently included in the same series specimens from different microhabitats. However, the combinations of specimens he collected in relatively small areas demonstrate the degree of sympatry existing among populations of these species, largely as a result of artificial clearing. The fact that a series of specimens taken in what the collector believes to be a very restricted locality or a uniform habitat may contain two of the three species and even rarely all three has not been generally recognized in the past and has been responsible for much confusion and many misidentifications. It should be emphasized that situations in which individuals of more than one of the three species are actually mixed together are unusual and almost always man-made. Some situations are misleading, such as when macropterous individuals of both *fasciatus* and *allardi* are attracted in great numbers to lights and remain temporarily in the immediate vicinity, even though only one of the two species is actually breeding there.

SEASONAL LIFE HISTORIES

In the Northern States all three species overwinter as eggs and mature in July, continuing to sing until the last individuals are killed by heavy frosts, generally in early November. These are among the last singing insects to survive as adults in this area, apparently because, as ground inhabitants, they are protected from brief periods of low temperature in deep grasses, crevices, and burrows, and under logs, boards, and stones. Their soft sounds become more and more obvious in late fall as other louder singing species are progressively killed off by early light frosts. In Ohio the earliest and latest singing dates for the three species are as follows: *fasciatus*, July 8-Nov. 14; *allardi*, June 29-Nov. 11; *tinnulus*, July 26-Nov. 18. Adults of the three species in the University of Michigan Museum of Zoology series were taken in central and northern localities on the following earliest and latest dates: *fasciatus*, July 17 (Marquette Co., Mich.)-Nov. 16 (Washtenaw Co., Mich.); *allardi*, July 23 (Mackinac Co., Mich.)-Nov. 26 (Urbana, Ill.); *tinnulus*, July 26 (Haywood Co., N. C.)-Nov. 6 (Washtenaw Co., Mich.). The chief difference in the life histories of the three species is that *fasciatus* probably has

two or three generations in the southeastern states (Fulton 1931), and breeds continuously in the Florida area. There are adults of *fasciatus* in the University of Michigan Museum of Zoology series taken every month of the year in Florida. The June 29 date for *allardi* is an unusually early date, from specimens taken in a sheltered southern exposure on the Ohio State University campus.

HYBRIDIZATION AND PROBABLE ISOLATING MECHANISMS

We have not conducted breeding experiments. Fulton (1933, 1937) was unable to get *fasciatus* to cross in the laboratory with either *allardi* or *tinnulus*, although he secured fertile offspring in stress matings between *allardi* and *tinnulus*. However, no one has ever reported hearing an intermediate song in the field, such as Fulton's hybrids produced. It is possible that an occasional hybrid is produced between these two species in the field, but there is no basis for assuming that such rare hybridization, even if it does occur ever results in gene flow between the species. Copulation between the two species is largely prevented in the field by the differences in their micro-distribution. It is likely that song differences and discordance in the sequence of male-female interactions during courtship in non-stress situations combine to complete isolation. The micro-distributional relationships of these two species and the extreme similarity between

the calling song of *tinnulus* and one of the courtship song rhythms of *allardi*, discussed in detail below, are of some interest.

Fasciatus and *allardi* probably never intercopulate in nature due to (1) a lack of inter-specific attraction at long range because of the radical differences between their calling songs, and (2) discordance during the courtship sequence when sexually responsive individuals happen into close proximity, perhaps largely due to differences in the courtship sounds. *Tinnulus* and *fasciatus* are almost totally isolated by differences in micro-distribution and this is also reinforced by radical song differences, both of these mechanisms operating prior to the physiological isolation demonstrated by Fulton's tests. The fact that *fasciatus* cannot interbreed with *allardi* or *tinnulus*, even under stress conditions, and the relatively great differences between the sounds of this species and those of *allardi* and *tinnulus* indicate that it is more remotely related to the latter two species than they are to each other. This relationship is also reflected in morphological characters.

MORPHOLOGICAL RELATIONSHIPS

The morphological relationships of the three species are confusing, as anyone who has tried to determine pinned material is well aware. We have examined thousands of specimens and have measured and plotted on various scatter diagrams a large number of characters. Those which most

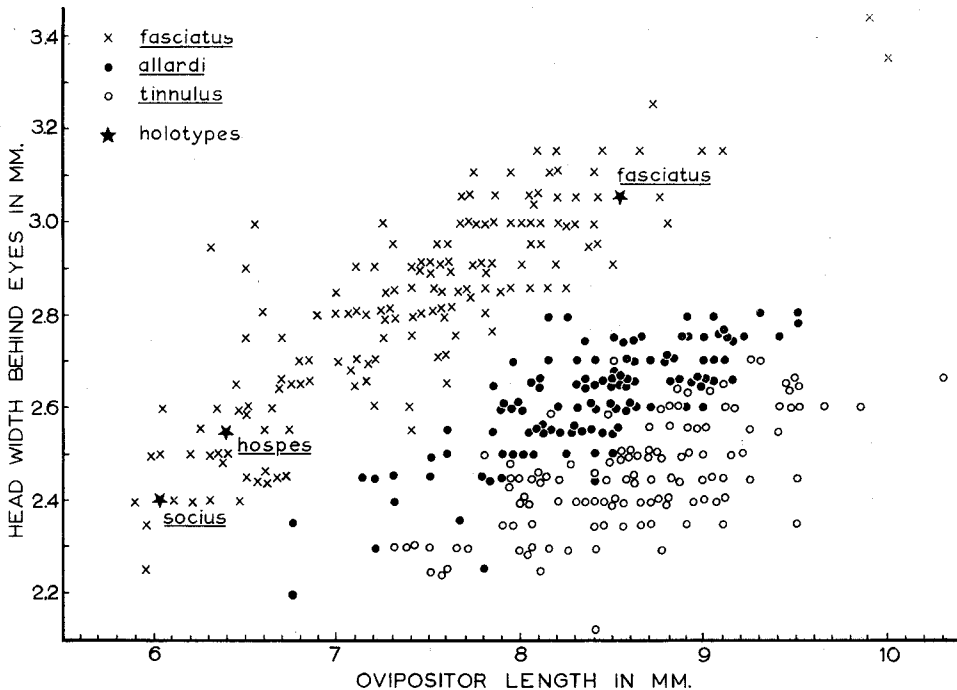


FIG. 3.—The relationship of head width behind the eyes to ovipositor length in females of species in the *Nemobius fasciatus* group. Specimens of each species are included from every state in which the species has been taken.

clearly separate the species are illustrated in figures 2 and 3. Our studies have revealed no new morphological characters by which to distinguish the three species, nor have they disclosed any single morphological character by which the species can always be separated. They have shown, however, that nearly all individuals of the three species can be separated by combinations of easily observed characteristics which have previously been considered to be of little value. Thus, as shown in figure 3, a high percentage of the females of the three species can be separated by plotting ovipositor length and head width behind the eyes on a scatter diagram. The males of *fasciatus* can be separated from those of the other two species by the short length of the stridulatory vein on the right tegmen, as viewed from above without dissection. In *fasciatus* the length of this vein from its median end to the inside edge of the ulnar vein (the ulnar vein connects to the stridulatory vein from the rear) is always less than 1.00 mm., and usually less than 0.90 mm., and is less than one-third as long as the width of the head behind the eyes. In *allardi* and *tinnulus* this part of the stridulatory vein is over 0.90 mm. in length, and this measurement is more than two-fifths the width of the head behind the eyes.

The general conformation and coloration of the head and pronotum (fig. 2) will allow confirmation of the identity of specimens which are still doubtful after ovipositor length or stridulatory vein length have been compared with head width. In *fasciatus* the head is broader and more fully rounded than in the other two species, and the pronotum in micropterous specimens is barrel-shaped, rather than trapezoidal as in micropterous specimens of the other two species. The dorsal head striping is nearly always intense in *fasciatus*, faint in *allardi*, and absent or nearly so in *tinnulus*. The dark lateral stripes on the pronotum are black in *fasciatus* and *allardi*, often only dark brown in *tinnulus*. The head and pronotum of *fasciatus* are usually strongly patterned in yellowish or buff and black. In *allardi* the pronotum is generally dark brown or nearly solid black, and the head is predominantly reddish-brown with darker brown or blackish markings less clear-cut. The head of *tinnulus* is usually sandy-reddish with scarcely any patterning at all, and the pronotum is light to dark red-brown with little or no patterning. As in *Acheta pennsylvanicus*, light-colored specimens of *N. allardi* occur in the Great Lakes region, and these may occasionally be confused with *tinnulus*.

The structure of the head and pronotum have previously not been recognized as good characters in this group, partly because of failure to recognize that differences appear in these structures between the macropterous and micropterous forms in *fasciatus* and *allardi*. As shown in figure 2, the rear border of the pronotum is widened in macro-

pterous specimens of *fasciatus* so that they take on a general appearance similar to that of the micropterous individuals of *tinnulus* and *allardi*. A similar change exaggerates this characteristic proportionately in macropterous specimens of *allardi*. Similar phase differences occur in *Acheta* (Alexander 1957b), and there are indications that characteristic differences in behavior are associated with these morphological differences. Of the three species, only *allardi* and *fasciatus* are known to produce macropterous individuals. *Tinnulus*, like *Acheta vernalis* (Blatchley), *A. fultoni* Alexander, and many other woods-inhabiting Orthoptera, is apparently always flightless. Over 1,000 specimens each of *fasciatus* and *allardi* were examined during the present study, and among these there were about 100 macropterous *fasciatus* and 250 macropterous *allardi*. Over 600 specimens of *tinnulus* were all micropterous. The situation(s) responsible for the production of macropterous individuals in crickets is unknown, but under certain circumstances macropterous *fasciatus* and *allardi*, as with *Acheta rubens* (Scudder), swarm to lights in tremendous numbers.

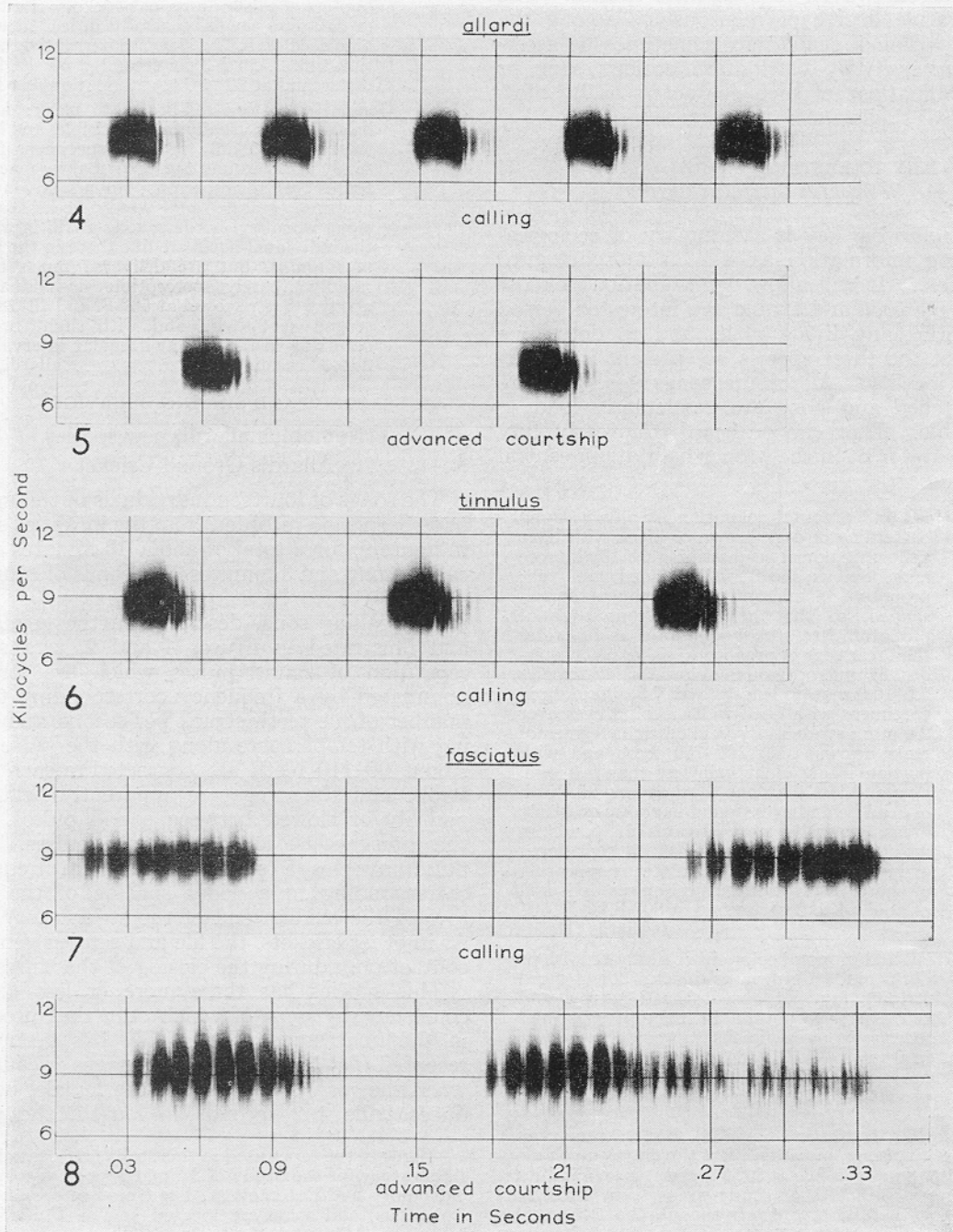
Positive separation of *fasciatus* males from the males of *allardi* and *tinnulus* can be made by removing the right tegmen and counting the number of teeth in the stridulatory vein. Counts by Fulton (1931), Pierce (1948), and the present writers give the following ranges in numbers of teeth on this vein in the three species: *fasciatus*, 101-145; *allardi*, 165-200; *tinnulus*, 187-239. The general appearance of the tegmina and of the stridulatory veins are respectively illustrated by Fulton (1931, p. 211) and Pierce (1948, pp. 122-123). *Allardi* and *tinnulus* have very similar stridulatory apparatus, the differences in their songs arising from differences in the rhythm with which the tegmina are stroked during sound production.

The inclusion of material from Western and Southwestern States in the three species under discussion has been another source of confusion in the study of morphological relationships in this group. As already stated, we believe that this material represents additional species. Its geographic location, outside most of the ranges of the three eastern species, almost completely precludes the possibility of its representing intergradation or interbreeding, even though certain of the characters of specimens from this area, such as ovipositor length and stridulatory vein length and number of teeth, are somewhat intermediate in nature.

While it is unfortunate that more satisfactory morphological distinctions have not been found among these species, it should be noted that such characters, especially if of a highly detailed or minute nature requiring dissection of every specimen or complicated measuring and statistical analysis, would probably not serve any important

taxonomic function. These three species can be separated perfectly well as living individuals, nearly all specimens can be distinguished on the pin, and there is no evidence of gene flow among them. Distribution records for the group can be compiled much more quickly by listening for songs than by examination of specimens, especially if dissection is required. If more than one specimen is included in material for which

identification is needed, and especially if ecological and song notes are included, determination becomes a minor problem. The relationships of the species are fairly clear. Morphologically ill-defined species are common among the singing Orthoptera, and are being discovered in more and more abundance in other groups of insects. There is no evidence that lack of distinctiveness in morphological characters alone is a criterion for



FIGS. 4-8.—Audiospectrographs of the songs of the *Nemobius fasciatus* group (figs. 4-5, at 80° F.; figs. 6-8, at 85° F.).

considering such species to be more recently diverged or related in any more unusual way than other closely related pairs and groups of species which exist in the same areas and are well defined by obvious morphological differences. The kinds of characters by which we visually distinguish specimens are not necessarily connected to sexual selection or to any other phenomena for which we should expect strong positive selection for divergence, even in sympatric species. The comparative degree of relationships among the species within a genus may sometimes be ascertained as easily by distribution, ecology, song, or by combinations of such characters as by morphological similarities.

KEY TO EASTERN SPECIES IN THE
Nemobius fasciatus GROUP

The following key is a summary of ecological and song information as well as morphological characters. It will allow determination of most pinned material and enable any interested person to identify any living male, and to determine which of the three species are present in a particular locality. All of the songs described are high-pitched and none are particularly loud or noticeable. They can be heard from early July until heavy frost in the proper habitats in central Ohio.

1. Head and pronotal coloration usually a strong patterning of dark brown or black with light yellowish; dorsal head striping usually intense and obvious; head well-rounded and full; pronotum in micropterous specimens barrel-shaped, so that head and front edge of pronotum are usually as wide as or wider than rear edge of pronotum; either macropterous or micropterous; ovipositor of females 5.9–10.0 mm. in length, over 7.5 mm. only in specimens with head width behind eyes over 2.6 mm.; stridulatory vein on right tegmen of male bearing only 100–150 teeth and with portion inside ulnar vein less than 1.0 mm. long and less than one-third as long as width of head behind eyes; found in grassy or weedy areas, generally near streams or ponds in moist situations, almost never on high slopes or in dry woodlands; song a steady repeating of short, buzzy, non-musical chirps delivered at about 4 to 9 per second at 80° F.²
fasciatus (DeGeer)
- 1¹. Head and pronotal color either sandy-reddish or dark reddish-brown or black; dorsal head striping faint or absent; head narrow and retracted; pronotum in micropterous and macropterous specimens trapezoidal, narrower in front so that head and front of pronotum are noticeably narrower than rear edge of pronotum; ovipositor of females 6.0 mm. to

10.3 mm. in length; head width behind eyes in females not over 2.8 mm.; stridulatory vein on right tegmen of males bearing more than 160 teeth, and with portion inside ulnar vein rarely under 1.0 mm. in length and more than two-fifths as long as width of head behind eyes; found in dry or moist grassy or weedy areas or in dry woodland; song a clear, musical, tinkling or trilling sound. 2

- 2 (1¹). General coloration pale and reddish, especially dorsal surface of head; macropterous specimens not known; found in and along the borders of oak-hickory, oak-hickory-chestnut, or oak-pine woods, generally in leaf litter or pine needles; song a slow uninterrupted "tink-tink-tink . . .," 2–3 per second at 50° F., 9–10 per second at 90° F. *tinnulus* Fulton
- 2¹. General coloration red-brown to black; dorsal head striping usually faintly visible, and head sandy-reddish only in some specimens from sandy areas around the Great Lakes; macropterous or micropterous; found in lawns, pastures, grassy, and weedy areas, rarely along woodland borders; song a trill in which the individual notes are like those in the song of *tinnulus*, but are delivered much more rapidly (barely perceptible individually), about 6–8 per second at 50° F. and 16–18 per second at 90° F., and with slight breaks occurring in the trill at irregular intervals of 2 to 30 seconds. *allardi*, n. sp.

SONGS AND SINGING BEHAVIOR³

Nemobius allardi, new species
Allard's Ground Cricket

The songs of fourteen individuals of this species have been tape-recorded from the localities shown in figure 9, for a total of about 13 minutes of the calling song and 3 minutes 30 seconds of courtship singing.⁴

The calling song, described in the key above and illustrated in figures 4 and 9, is a simple repetition of sound pulses which are strongly dominated by a frequency corresponding to the number of file teeth struck per second and varying with temperature along with the pulse rate. About 90–110 teeth are contacted in each wing-stroke and the wings are apparently held temporarily or slowed between sound pulses, since the intervals are longer than the pulses. Each pulse involves a slight downslur in frequency corresponding to a wider spacing of the teeth toward the median end of the stridulatory vein. As in other crickets, the file and scraper generally contact only during the closing of the wings.

This species has three more or less distinct courtship rhythms, of which only that produced in the final stage of courtship has been tape-recorded (fig. 5). In the early stages of courtship when the male is still facing the female, he produces trills 1–2 seconds in length, the pulses

²*Miogryllus verticalis* (Serville) has a remarkably similar calling song, but it delivers the chirps much more slowly, 1 to 8 in 5 seconds at 80° F., and it is an inhabitant of dry grassy hillsides or sandy areas, very rarely occurring together with *fasciatus* though the two species have similar geographic ranges. The songs of eastern *Miogryllus* will be discussed and compared with those of *fasciatus* in a later paper.

³Some of the tapes used in this study are located in the Laboratory for the Study of Animal Sounds, Department of Zoology and Entomology, The Ohio State University, Columbus, and some are located in The University of Michigan Museum of Zoology. The recording and analyzing equipment used was that described by Alexander (1957).

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 the trill. This stage of courtship is probably analogous to the precourtship phase in *Acheta* described by Alexander (1957). When courtship has advanced somewhat and the male has reversed his position

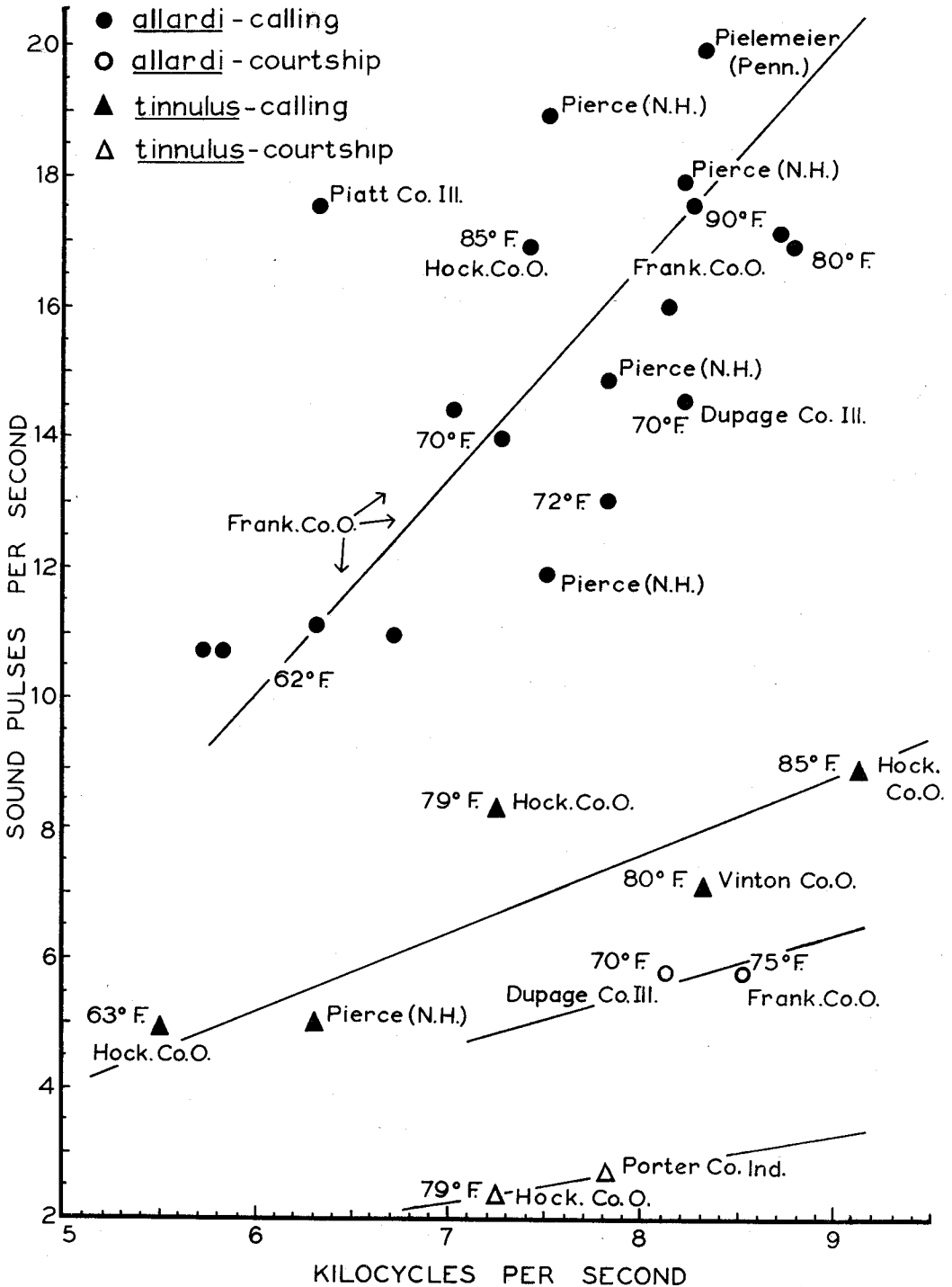


FIG. 9.—Scatter diagram of pulse rate and frequency at various temperatures in the calling and courtship songs of *Nemobius allardi* and *N. tinnulus* from different localities (lines are approximate). Pielemeyer (Penn.) and Pierce (N. H.) are literature records from Pielemeyer (1946) and Pierce (1948).

and begun to back toward the female's head, a slower pulse rate of 5 to 6 per second is produced, and the pulses are grouped 4 to 8 in a series with breaks of a fraction of a second between series. Sometimes this song develops into a uniform slow tinkle as courtship advances (fig. 5), resembling the calling song of *tinnulus* (fig. 6). In these last two songs the male jerks his body each time a group of pulses is produced, or shakes his entire body during the ungrouped pulse sequence. The ungrouped, slow pulse sequence is probably analogous to full courtship in *Acheta*, and the intermediate rhythm to the mixed courtship of *Acheta* (Alexander 1957).

Fulton (1931, 1933) described both the calling song and the courtship songs of this species from several different localities. His estimates of the pulse rate in the calling song are as follows: Iowa, 5–6 per second at 50° F., 8–9 per second at 61° F.; North Carolina Mountains, 7 per second at 60° F., 8 per second at 66° F., 9 per second at 68° F., "Specimens from Raleigh, North Carolina appear to have a slightly higher rate than the mountain specimens." (1931, p. 222). In 1933 he gave the range of pulse rate in this species from 5 per second at 50° F. to 15 per second at 80° F. A comparison of these figures with those in figure 9 shows that they are all slightly lower. Pielemeier (1946) gave a pulse rate of 20 per second for this species (no temperature indicated) at University Park, Pennsylvania, 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). Pierce (1948) noted pulse rates varying from 14.5 to 20 per second in New Hampshire at temperatures ranging from 69.4° F. to 96.8° F., and gave the dominant frequency in a song delivered at 19 pulses per second as 7500 cycles per second. These estimates are somewhat higher in pulse rate than those found in the present study, both for a given temperature and for a given frequency. Pierce also estimated that 162 to 172 teeth were struck per pulse, a higher figure than that obtained in the present study.

Neomobius tinnulus Fulton

The Tinkling Ground Cricket

The songs of four specimens of this species have been tape-recorded from the localities indicated in figure 9, for a total of about 9 minutes of the calling song and 70 seconds of courtship singing.⁵

⁴Tape recordings made of the songs of five individuals from Greenbrier Co., W. Va., Washington Co., Va., Swain Co., N. C., Blount Co., Tenn., and Jefferson Co., Ala. by T. E. Moore and K. C. Shaw became available as the manuscript was being sent to press. They are not included in fig. 9; all but the last are shown as song records in fig. 1.

⁵Tape recordings made of the songs of two individuals from Tuscaloosa Co., Ala., and Scott Co., Miss., by T. E. Moore and K. C. Shaw are included in fig. 1, but not in fig. 9.

Several courtship sequences have been watched in cages and two different rhythms were observed at different stages of courtship. When a male first approaches 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 position, stops jerking, and backs toward the female while producing a regular succession of pulses at a rate of about 3 per second, at 80° F. This is the only courtship song which has been tape-recorded. During this sequence the body of the male shudders rapidly, as was described for *N. allardi* in full courtship. This is the courtship song most often heard from a culture, probably because more time is spent in this stage of courtship than in the other preliminary phase. In one case a male singing the calling song was noticed to be approached from the rear by a responsive female, and the less commonly heard rhythm was completely omitted.

As shown in figures 4–6, the individual pulses in the songs of *tinnulus* and *allardi* are practically identical. The only differences in the songs are in the rate and rhythm of delivery of these pulses, and in these characters the modifications in the songs of each of the two species from one situation to the next are also analogous. In each case *tinnulus* delivers pulses more slowly than *allardi*, and the full courtship singing of *allardi* is very similar to the calling song of *tinnulus*. The differences between the songs of the two species, and between the different songs of each species, are the result of variations in the length of the intervals between pulses. The two species have very similar stridulatory veins and they strike about the same number of teeth per sound pulse. The pulse intervals in the calling song of *tinnulus* and in the courtship songs of *allardi* are longer than the pulses, indicating that the wing motion is not continuous, but involves a brief period between successive sound pulses during which the wings are held motionless. This "hold" is obvious to the unaided eye. Fulton (1933) crossed *allardi* and *tinnulus* and found that the resulting hybrids had pulse rates (wing "hold" intervals) intermediate between those of the two parents. Backcrosses with the two parents moved the pulse rate in the F₂ hybrids part way toward that of the parent used in the backcross. This example and the song of a presumed hybrid *Acheta* described by Alexander (1957b, p. 598) are apparently the only instances in which there is some suggestion as to how interspecific song differences are inherited in crickets.

Fulton (1931) described the calling song of *tinnulus* and says that in the courtship song the pulses are produced about half as fast as in the calling song. His estimates of the pulse rate in the calling song are as follows: Iowa, 7–8 per

second at 80° F., 5-5.7 per second at 66° F., 4.4 per second at 65° F., 4.3-5 per second at 61° F., 3.8 per second at 59° F.; Raleigh, North Carolina, 7 per second at 82° F., 8 per second at 79° F., 7 per second at 75° F., 6 per second at 69° F., 5.5 per second at 67° F., 5 per second at 66° F., 4 per second at 66° F. Pierce (1948) gives the pulse rate as 5-10 per second with the dominant frequency of the sound at 6.3 kilocycles per second at a pulse rate of 5 per second. He estimated that 126 teeth were struck during each sound pulse. All of these figures agree well with those obtained in the present study.

***Nemobius fasciatus* (DeGeer)**

The Striped Ground Cricket

The songs of eleven individuals of this species have been tape-recorded from Adams and Licking Cos., Ohio; Bourbon Co., Ky.; Greenbrier Co., W. Va.; Yazoo and LeFlore Cos., Miss.; LaFourche Parish, La.; and Dade and Sarasota Cos., Fla., for a total of about 10 minutes of the calling song and 4 minutes of courtship singing.

The calling song of this species is a continuous repeating of high-pitched, soft, buzzy, multipulse chirps, each lasting a little less than a tenth of a second. Each chirp in the calling song contains 7 or 8 pulses and each pulse contains about 30 toothstrikes. The chirp rate is usually 2-4 per second at 75-85° F. The file of this species contains fewer teeth than those of *allardi* and *tinnulus*, but the teeth are spaced the same at similar locations on the file. *Fasciatus* uses only about a third as many teeth as do *allardi* and *tinnulus*, and the pulses in its chirp are about a third as long. The songs of *fasciatus* and of *Miogryllus* species sound considerably less musical to the ear than the songs of *allardi* and *tinnulus*, but when played at a reduced speed, lowering the frequencies, they sound nearly as clear and musical as the songs of other crickets. The failure of the ear to note the dominant pure frequency is probably partly due to the high frequency involved, and partly due to the nature of the song rhythm. It is amazing that sounds as different as those of *allardi* and *tinnulus* are from that of *fasciatus* can be produced with stridulatory structures which are so similar.

In the early stages of courtship in this species, the calling song is modified by an increase in the chirp rate up to 8 to 12 chirps per second, a decrease in the number of pulses per chirp to 2 to 5, and a decrease in the intensity of the dominant frequency. In a later stage of courtship the singing rhythm changes so that the chirps are produced in groups of 3-6 with the last chirp in each group a little longer, its pulse rate a little slower, and its pitch dropping a little toward the end of the chirp. Figure 8 shows the last two chirps in such a group. The male jerks his body backward at the end of the last chirp in each group.

Fulton (1931, 1932) noted the following chirp

rates in the calling song of this species: Ames, Iowa, 2.5-3 per second at 77° F., 4 per second at 80° F.; Raleigh, North Carolina, 7 per 5 seconds at 66° F., 3-5 per second at 86° F., 4-6 per second at 88° F.; Ripley, West Virginia, 3 per second, probably over 90° F.; Geneva, N. Y., 3-5 per second, over 80° F. Fulton also described the courtship rhythms discussed above, and observed 5-9 pulses per chirp in early courtship.

Pierce (1948) found a chirp rate of 1.4-5 per second in Franklin, New Hampshire, specimens, 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 (no temperature given). He estimated that 56 of 118 teeth were used per pulse.

A male encounter or fight chirp noted in this species involves an increase in the number of pulses. The same kind of sound is produced by males of *Miogryllus* and *Acheta* in the same situation. As already noted, the different sounds of *N. fasciatus* are surprisingly like those of *Miogryllus verticalis* in spite of the fact that these two species are placed in different subfamilies. The sounds of these two species do not closely resemble those of any other crickets in the eastern United States. The significance of their striking similarity to each other is not known.

DISCUSSION OF MALE COURTSHIP BEHAVIOR

The courtship behavior of male crickets can generally be divided into three stages on the basis of more or less obvious changes in (1) the type of sound being produced, (2) the character of the body maneuvers, and (3) the relative positions of the male and female. These three stages can be described as follows: (1) preliminaries of short duration performed while the male is facing the female, (2) an intermediate stage sometimes lasting several minutes during which the male reverses his position and makes distinctive sounds and movements with his posterior end directed toward the female's head, and (3) advanced courtship, which is usually of relatively short duration and is characterized by the male actively promoting contact with the female and assumption of the copulatory position. In crickets, the female mounts the male in copulation and the activity of the male in this final stage consists of flattening his body against the substrate, backing toward the female until contact is established, then either backing under the female or simply allowing her to mount. The nature of the final phase of courtship depends on the responsiveness of the female. If she withdraws upon contact, the male generally resumes the activities characteristic of the intermediate stage of courtship, and if her withdrawal is more pronounced, he is likely to stop courting, turn around and face her, and begin the preliminaries again. If she leaves, the male in some species

produces distinctive sounds similar to those produced during encounters with other males. There are, of course, variations in the courtship patterns of different species, some species producing no sound at all during courtship, others producing only a single sound during only one of the phases of courtship. In general, when female-attracting glands are present (e.g., *Oecanthus* spp.), courtship sounds are intermittent and not distinctive; when such glands are absent (e.g., *Acheta*, *Miogryllus* spp.), courtship sounds are rhythmic, continuous, and distinctive.

Courtship phases (2) and (3) above probably correspond to Gabbutt's (1954) Phases II and III in the courtship of *Nemobius sylvestris* (Bosc.). Gabbutt does not describe a preliminary or encounter phase, described as (1) above. His Phase I refers to situations in which the calling song is produced.

The chief difference between the courtship of Nemobiinae and that of Gryllinae is that in the latter a distinctive, more or less continuous, tegminal rhythm is produced during the final stage of courtship, and this rhythm is so similar in different species of *Acheta* and *Gryllus*, and in *Gryllodes sigillatus* (F. Walker) that a common origin is suggested. None of the Gryllinae are known to possess a dorsal gland or other structure attractive to the female and involved in inducing her to assume the copulatory position. Apparently all of the Nemobiinae possess such a gland, at the base of a spine on the hind tibiae in American species (Fulton 1931; Gurney 1947) and on the right tegmen in European species (Richards 1952). Neither *Nemobius* species nor *Miogryllus* species have courtship songs of a nature which suggests a common origin with those known in *Acheta*, *Gryllus*, *Gryllodes*, and *Anurogryllus* (Alexander 1956, 1957, and unpublished data). There are indications that small groups within the Nemobiinae have courtship songs derived from a single source (*allardi* and *tinnulus*; *carolinus* and *melodius*—see Alexander 1957a), but there is no evidence for a common origin of the courtship songs of all Nemobiinae.

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