THE SONG RELATIONSHIPS OF FOUR SPECIES OF GROUND CRICKETS

(ORTHOPTERA: GRYLLIDAE: *NEMOBIUS*)[1]

RICHARD D. ALEXANDER

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

INTRODUCTION

Several accounts have been written of the mating behavior of different species of ground crickets (Fulton, 1931; Richards, 1952; Gabbutt, 1954), and many excellent descriptions of their songs, based on auditory impressions, have appeared (Fulton, 1930, 1931, 1932; Cantrall, 1943; and many others). A few song analyses have been made with mechanical or electronic devices (Fulton, 1933; Pielemeier, 1946, 1946a; Pierce, 1948). Detailed comparative studies of song relationships in the singing Orthoptera and Cicadidae are almost non-existent, though it is increasingly apparent that satisfactory interpretations of the taxonomic and distributional relationships of these species will depend on such studies.

The present investigation is based on laboratory and field observations, and on tape recordings of songs analyzed by means of a Vibralyzer. The species discussed include *Nemobius carolinus carolinus* Scudder, *N. confusus* Blatchley, and *N. melodius* Thomas and Alexander, the only eastern representatives of the subgenus *Eunemobius* Hebard. A fourth species, *N. maculatus* Blatchley, belonging in the subgenus *Allonemobius* Hebard, is also considered here because of certain distributional and song relationships with the above species.

The recordings used for song analysis are deposited in the Library of Animal Sounds, Department of Zoology and Entomology, The Ohio State University. They were made with a Magnemite, Model 610-E (in the field) and a Magnecorder, Model PT6A (in the laboratory) at a tape speed of fifteen inches per second. American Microphone Company Microphones, Models D-33 and D-33A, were used, both in the field and in the laboratory. Explanations of the Vibralyzer and its uses can be found in Borror and Reese (1953) or Alexander (1956, 1957).

Crickets in the genus *Nemobius*, as well as other ground-inhabiting crickets in general, produce the calling song both day and night, though usually more individuals in a colony are involved in song at any particular time at night than at any time during the day. None of the ground crickets are known to synchronize or alternate the periodical elements of their songs as do species in several different genera and subfamilies of Tettigoniidae and Gryllidae which live on vegetation.

Aside from the calling song, many *Nemobius* species produce variously distinctive and complex sounds during courtship and during encounters between males. Apparently all *Nemobius* species possess some sort of female-attracting gland, in American species at the base of the spine on the hind tibiae, and in European species on the right tegmen (Fulton, 1931; Richards, 1952, 1953). Some species have not been heard to produce sounds during courtship, and in others there is only intermittent sound production at wide intervals, such as occurs in most of the tree crickets (Oecanthinae) which possess a highly developed metanotal gland. In *Nemobius* species as well as other crickets, jiggling and jerking of the

[1]This study has been supported by grants from The Ohio State University Development Fund, the Graduate School of The Ohio State University, and the Rockefeller Foundation. The author is indebted to Dr. Edward S. Thomas of the Ohio State Museum and Dr. Donald J. Borror of the Department of Zoology and Entomology of The Ohio State University for advice and assistance.

body during the various stages of courtship, in time with the courtship song if one is produced, suggests that rhythm sometimes operates as a visual stimulus in courtship.

Key to the Calling Songs of Species Compared Here
(Based on characteristics apparent to human ears)

1. More or less continuous trills, or rapid successions of sound pulses, usually lasting several minutes without perceptible breaks 2

1'. A rhythmical succession of short trills, 3–5 delivered in 5 seconds, each trill lasting ½ to 1 second, beginning softly and increasing in intensity, then ending abruptly. Sometimes short, detached portions occur before or after each trill, or the first part of the trill is rather jerky or pulsating . . . . *Nemobius confusus* Blatchley

2(1). A smooth, clear (musical), high-pitched, continuous trill in which the individual sound pulses (each caused by a single wingstroke) are perceptible, but far too rapid to count . . . . *Nemobius melodius* Thomas and Alexander

2'. Jerky or pulsating trills, rarely smooth, and in such cases the individual sound pulses are delivered so rapidly that they are individually completely imperceptible and a buzzing or droning effect is created 3

3(2'). A jerky trill in which the catches occur regularly at about 3–8 per second (depending on temperature) . . . . *Nemobius maculatus* Blatchley

3'. A buzzing or droning trill which may take one of the following three forms; (a) a pulsating trill in which rapid pulsations are delievered at 10–13 per second (rare), (b) a smooth trill completely lacking in pulsations perceptible to the ear (rare), or (c) a trill which consists of an alternation of (a) and (b) at a rate of 1–3 cycles in two seconds, and with the intensity reduced during the smooth phase of the cycle (most common of the three forms) . . . . *Nemobius carolinus* Scudder

Nemobius melodius *Thomas and Alexander*[2]

The Melodious Ground Cricket

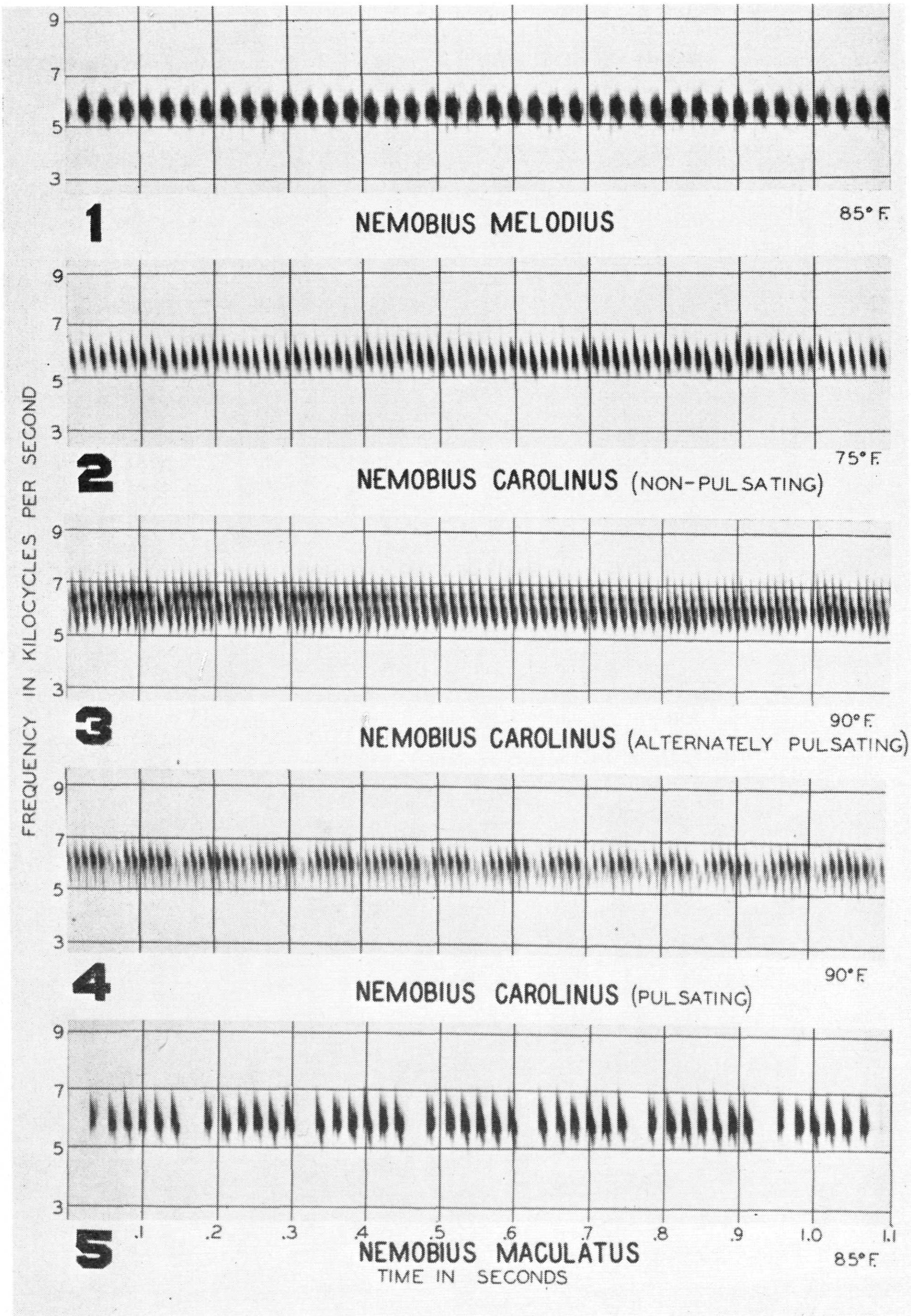
The songs of six individuals of this species have been recorded, four from Licking County, Ohio (two in the laboratory and two in the field), and two from Carroll County, Ohio (one in the laboratory and one in the field). A total of 25 minutes and 42 seconds of the calling song was recorded. A male caged with several females was recorded for 4 minutes and 38 seconds, and during this time he produced 12 brief bursts of song (fig. 6) which resemble closely a short trill that males of *carolinus* produce around females, and which is probably associated with courtship. This short trill is also structurally similar to the individual trills in the calling song of *confusus* (fig. 7 to 9). This type of song relationship—the calling song of one species being similar to the courtship song of a closely related species—also occurs between *N. fasciatus* (DeGeer) and *N. tinnulus* Fulton. The short trills of *carolinus* and *melodius* are the only courtship sounds noticed in any of the species discussed here, and their simplicity and infrequent production indicates that their function in courtship is probably slight.

The calling song of *melodius* is compared to those of *carolinus* and *maculatus* in figures 1 to 5. When undisturbed, an individual producing the calling song strokes the tegmina fairly continuously and evenly, often for several minutes at a time. However, when disturbed, or when changing position (this latter some-

[2]The songs of this species were erroneously attributed to *N. palustris* Blatchley and to "*Anaxipha*? undescribed" by Alexander (1956) (pp. 146–148; 204–205; figs. 89, 94, 111).

EXPLANATION OF FIGURES IN PLATE I

1. Calling song of *N. melodius*.
2. Non-pulsating calling song of *N. carolinus*.
3. About one cycle of the alternately pulsating calling song of *N. carolinus*.
4. Pulsating calling song of *N. carolinus*.
5. Calling song of *N. maculatus*.


FREQUENCY IN KILOCYCLES PER SECOND
9
7
5
3
1
NEMOBIUS MELODIUS
85° F.
2
NEMOBIUS CAROLINUS (NON-PULSATING)
75° F.
3
NEMOBIUS CAROLINUS (ALTERNATELY PULSATING)
90° F.
4
NEMOBIUS CAROLINUS (PULSATING)
90° F.
5
NEMOBIUS MACULATUS
85° F.
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
1.1
TIME IN SECONDS

times occurs frequently); a singing male introduces almost imperceptible breaks into his song, sometimes involving the deletion of only one or two pulses. In addition, he may slow the rate of tegminal motion, at the same time lowering the intensity of the sound slightly. These traits are also characteristic of the songs of *carolinus* and *confusus* and serve as recognition characters for the songs of species in the subgenus *Eunemobius*. In both *carolinus* and *confusus*, however, these fluctuations in intensity and pulse rate have become rhythmical elements in the song. In *melodius* they occur at irregular intervals, and without any consistent pattern.

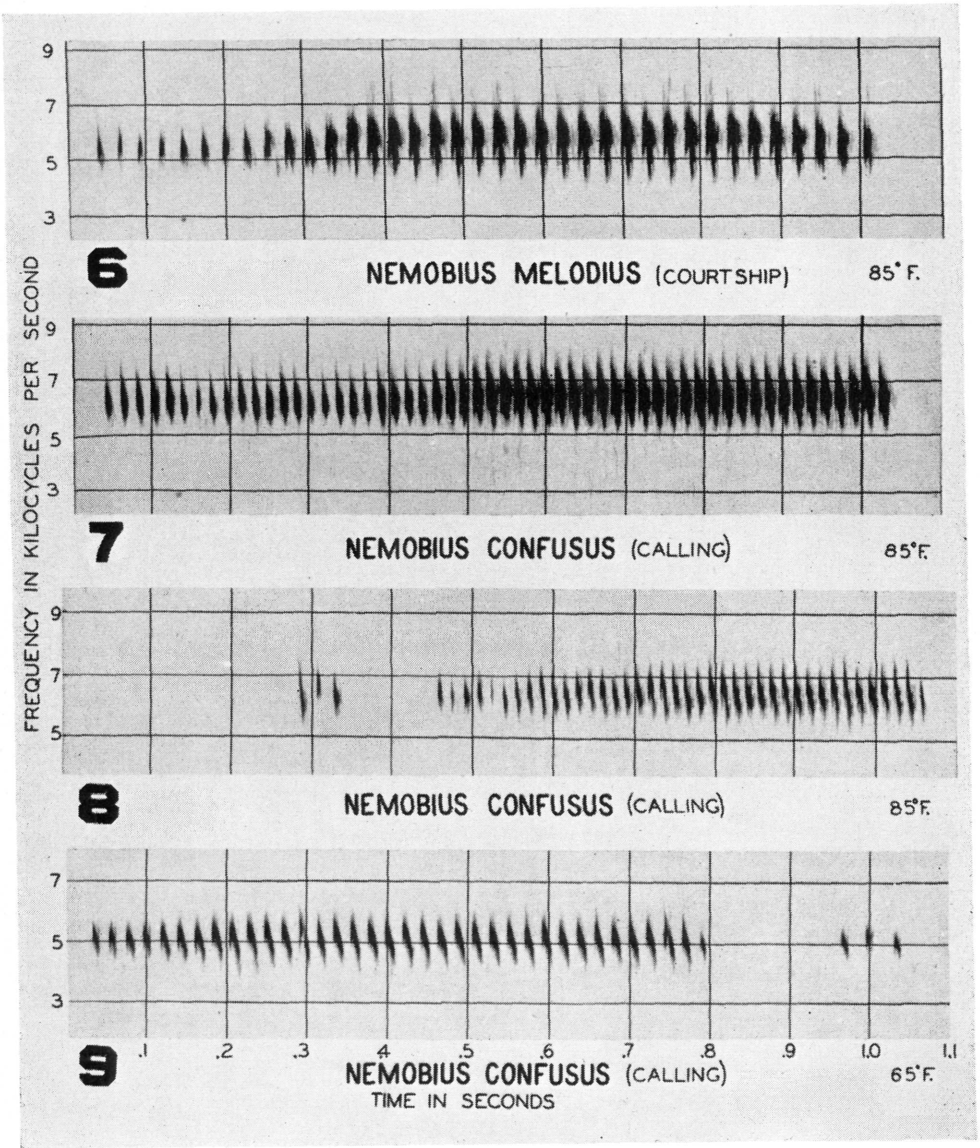
As shown in figure 10, the calling songs of *carolinus* and *melodius* differ considerably in pulse rate at the same temperature and frequency. Each symbol in the diagram represents the song of a different individual, analyzed from audiospectrographs of one second or more of the song. The frequency determinations are averages of five readings made from section Vibragrams (intensity versus frequency) of the same second of song. A comparison of recordings of one individual each of the two species from Carroll County, Ohio, made at 78 and 79° F, respectively, shows that the songs are pitched at about 5.6 and 5.8 kilocycles per second. However, the song of *melodius* at this temperature has a wingstroke rate producing 34 pulses per second, while *carolinus* produces 75 pulses per second.

The dominant frequency in cricket songs has usually been considered to correspond to the number of teeth on the stridulatory vein or file that are struck per second (Lutz and Hicks, 1930; Alexander, 1956). Thus, a difference in pulse rate can either be due to a difference in the actual speed of motion of the tegmina (distance travelled per unit time), to a difference in the length of the stroke, or to a combination of these factors. In the first case there should also be a difference in the frequency caused by the rate of file toothstrike, providing the file teeth are spaced the same in both species; in the second case the toothstrike rate would be the same in the two species.

It is difficult to make an exact comparison of the teeth per unit space on the file since this varies, the teeth being progressively more widely spaced toward the lateral end of the file (fig. 1, Thomas and Alexander, 1957). This differential spacing is probably reflected in the downslurring in frequency which can be detected in each pulse in cricket songs. This downslurring might also be attributed to a drop in speed of motion of the tegmina during file-scraper contact. However, when brief contact of the file and scraper occurs on the "backstroke" (probably the opening of the tegmina), a slight rise in frequency occurs, indicating that file-tooth spacing is probably the important factor.

Due to the downslurring of each sound pulse and the differential spacing of the file teeth (and since we do not know exactly what portion of the file is involved in sound production), it is difficult to make an exact correlation between frequency and file spacing. However, by expanding audiospectrographs timewise, counts can be made of the number of teeth struck during each sound pulse. Such counts in several pulses of the songs of two specimens recorded from Carroll County, Ohio, at 78 and 79° F, showed that *carolinus* used 25–33 file teeth per sound pulse, while *melodius* used 57–73. This difference indicates that the pulse rate differences between the songs of the two species chiefly involves a difference in the length of the stroke of the tegmina rather than in the actual speed of their motion. The difference in number of teeth struck per sound pulse is correlated with the actual number of teeth in the file which ranged from 51 to 63, in 14 individuals of *carolinus*, and 110 to 127, in 7 individuals of *melodius*.

A number of morphologically ill-defined species have been revealed in the singing Orthoptera (Fulton, 1931, 1952, 1956; Alexander, 1956, and unpublished data) which have song differences of varying degree. It is often assumed that these song differences should be reflected in differences in the external sound-



EXPLANATION OF FIGURES IN PLATE II

6. Presumed courtship trill of *N. melodius.*

7, 8, and 9. Single trills from the calling song of *N. confusus.*

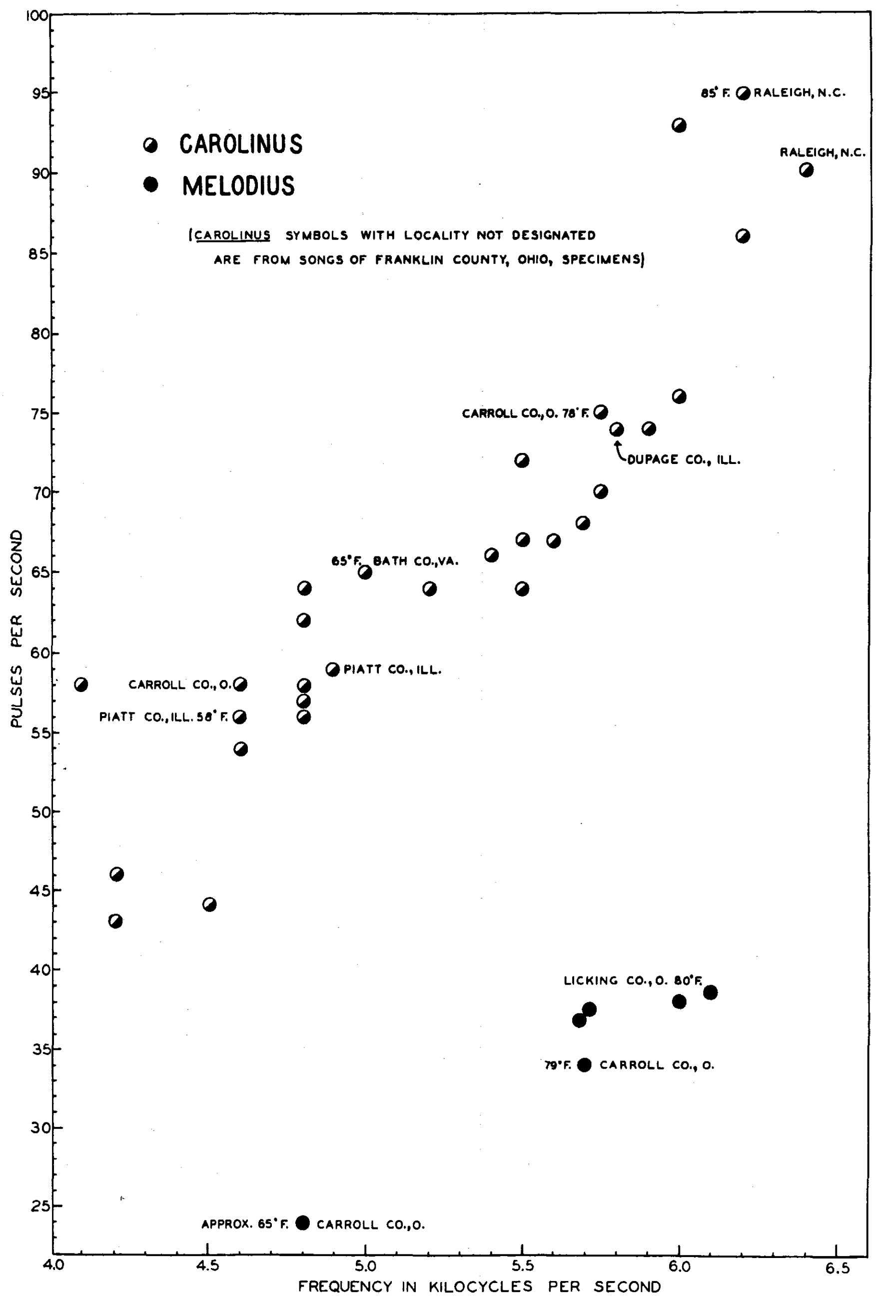


FIGURE 10. A comparison of pulse rate and frequency in the calling songs of *Nemobius carolinus* and *N. melodius* recorded at different places and at different temperatures.

producing structures. In such cases, however, the song differences are chiefly or entirely differences in rhythm. The length of the file and the spacing of its teeth are probably the only characters in which taxonomists can expect to find differences correlated with differences in the song rhythms of closely related species. In most cases, rhythm differences do not involve the external sound-producing structures in any way.

Nemobius carolinus *Scudder*

The Carolina Ground Cricket

Twenty-nine individuals of this species were recorded from the localities indicated in figure 10, for a total of 11 minutes and 5 seconds of the calling song.

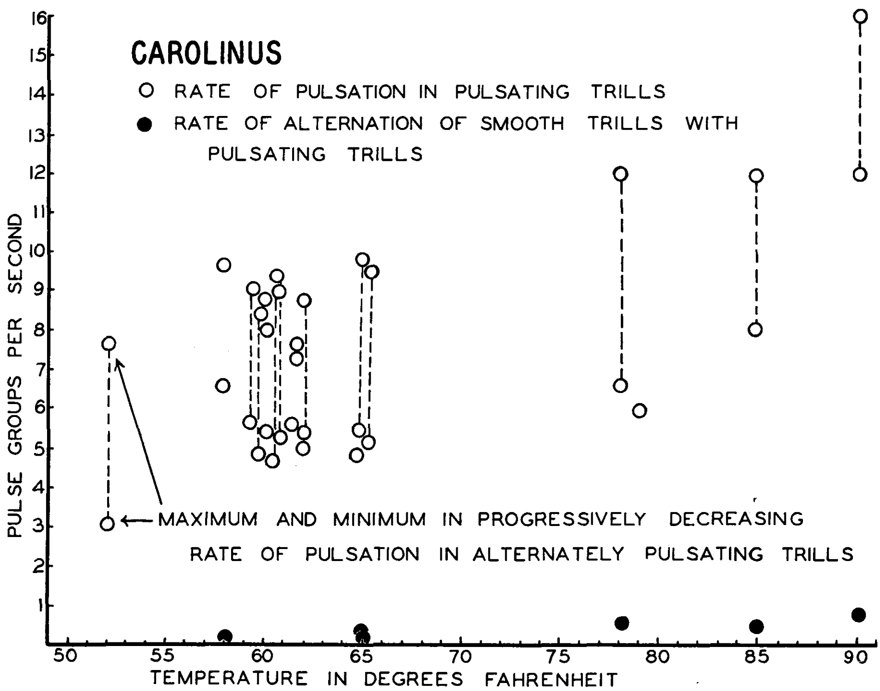
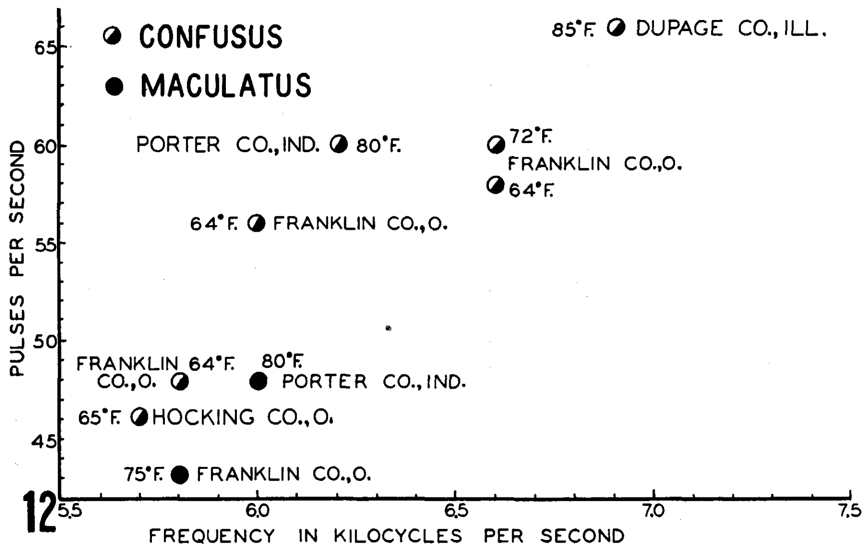


FIGURE 11. The rates of delivery of rhythmical elements superimposed on the basic pulse rate in the calling songs of *Nemobius carolinus* recorded at different temperatures.

The short trills produced around females and probably connected with courtship were heard on several occasions both in the laboratory and in the field, but no recordings were obtained.

The calling song of *carolinus* is a continuous trill resembling that of *melodius* in the characteristics mentioned above. However, considerable variation occurs in the recorded songs attributed to this species, with respect to the presence or absence and regularity of changes in intensity and pulse rate (see key above). The most commonly heard song involves an alternation of two types of trills, one smooth and the other pulsating as a result of every 6th to 8th pulse being de-emphasized (fig. 3). The complexity of this song is further increased by a progressive decrease in the rate of pulsation (progressive increase in the number of pulses between de-emphasized pulses) during each pulsating phase or cycle. Progressive changes of this sort occur frequently in the more complicated insect songs, and are often quite consistent, suggesting possible behavioral significance. In addition to the alternately pulsating type of trill, some individuals always damp every sixth or seventh pulse (fig. 4), and others trill evenly all the time (fig. 2). These variations cannot be correlated with geographic locality or habitat, and the two extremes may occur in the songs of individuals collected only a few feet apart. A few of the recordings are of individuals which have imperfectly or irregularly pulsating songs that may be intermediates. No differences in pulse rate or



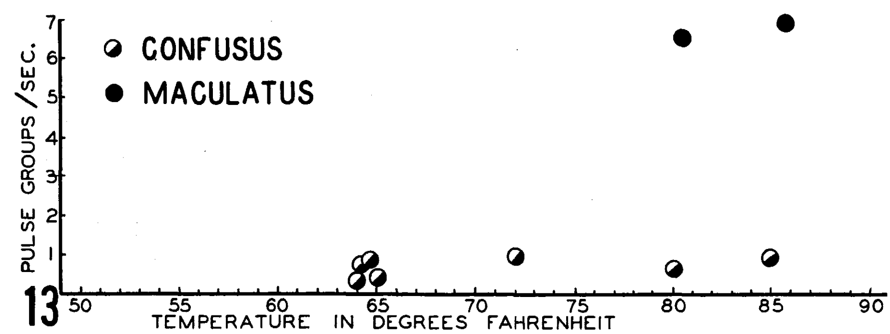


FIGURE 12. A comparison of pulse rate and frequency in the calling songs of *Nemobius confusus* and *N. maculatus* recorded at different places and at different temperatures.
FIGURE 13. The rates of delivery of pulse groups in the calling songs of *Nemobius confusus* and *N. maculatus* recorded at different temperatures.

frequency have been found between the three types of song, and it seems likely that this is infraspecific variation, and that it is of genetic origin rather than associated with variations in the stimulus situation.

As shown in figure 10, the pulse rate in the songs of all individuals recorded varies from 43 to 95 per second, and the frequency varies from 4.2 to 6.4 kilocycles per second over a temperature range of about 50 to 90° F. Figure 11 shows that the rate of pulsation due to the damping of occasional pulses is quite variable, and ranges from 3 to 16 per second. The rate of alternation of pulsating and non-pulsating cycles varies from 5 to 44 cycles per minute.

Cantrall (1943) gives a detailed description of the song of Michigan specimens which corresponds closely to that given above for the alternately pulsating trill. He says the complete cycles of pulsation and non-pulsation occur about 24 times a minute. Fulton (1931) gives the same description for specimens from Iowa and North Carolina, adding (p. 226), "Rarely males will be heard that seldom sing without beats, but usually there is a regular repetition of the two phases of the song, sometimes one second for each period and sometimes longer. Sometimes when starting to sing this species will sound a few notes which increase in volume and then die out." Pierce (1948, New Hampshire) obtained a frequency of 5430 cycles per second at 70 pulses per second from analysis of a pulsating song in which every 6th to 8th pulse was de-emphasized. These figures agree well with those obtained here.

Nemobius confusus *Blatchley*

The Confused Ground Cricket

Seven individuals of this species were recorded, from the localities indicated in figure 12, for a total of 6 minutes and 24 seconds of the calling song. No other sound has been heard. The calling song consists of a succession of short trills, each lasting ½ to 1 second and occurring at rates of 2–5 in 5 seconds. Each of the trills begins rather softly and increases gradually in intensity until it ends abruptly. Some individuals preface each trill with 1–4 short, soft pulsations (fig. 8), sometimes completely detached from the rest of the trill. Sometimes these detached portions seem to come after the trill rather than before it (fig. 9). The individual trills in this song, as mentioned above, closely resemble the short trills produced by *carolinus* and *melodius* during courtship (*cf.* fig. 6 and 7). This song is also more closely related to the calling song of *carolinus* than would seem in a superficial comparison. If the intervals between trills were cut out, the result would be a more or less continuous trill similar in structure to the alternately pulsating trill of *carolinus*. In the song of one specimen of *confusus*, there are places where the trills are run together, causing it to sound very much like *carolinus*.

As shown in figure 12, the pulse rate in the calling song of *confusus* varies from 46 to 66 per second, and the frequency varies from 5.7 to 6.9 kilocycles per second between 64 and 85° F. In ten trills analyzed, there were from 36 to 56 pulses per trill.

This song has apparently been described only by Fulton (1931, 1932) who observed specimens which attached 2 and 3 of the brief pulsations to the front of the trill. He gives trill rates as follows: Iowa, 70° F, 1–2 per second; Raleigh, North Carolina, 75° F, 9–10 per 10 seconds, and 80° F, 10–13 per 10 seconds.

Nemobius maculatus *Blatchley*

The Spotted Ground Cricket

Two individuals of this species were recorded from the localities indicated in figure 12, for a total of 3 minutes and 40 seconds of the calling song. No other sound was noticed in cultures containing both males and females.

The calling song is a rather soft, continuous trill with a regular "skip" occurring at a rate of about 6.8 per second at 85° F. As shown in figure 5, this skip is a slight gap after every 6th or 7th pulse, as if one pulse had been left out. The pulse rate within pulse groups was 43 and 48 per second in the two specimens recorded, and the frequency of the two songs was 5.8 and 6.0 kilocycles per second, respectively (fig. 12).

The pulsating trill of *carolinus* bears an interesting relationship to this song, since it has every 6th to 8th pulse de-emphasized, or softer than the others. If the beat caused by this damping of every 6th to 8th pulse is behaviorally significant, one can easily imagine an accentuation of this character by the complete loss of this pulse. It would be interesting to know if *maculatus* strokes its tegmina silently during the skip in its song, or holds or slows them momentarily. *N. maculatus* and *carolinus* are not closely related, and it is unlikely that the song of one is derived from a song immediately ancestral to the other. However, comparison of the songs of *carolinus*, *maculatus*, and *confusus* illustrates two possible methods of transition from a trilling or continuous monorhythmic song to a dirhythmic chriping song (very short pulse groups produced at long intervals, such as in *Acheta*).

The song of *maculatus* has been described by Fulton (1931) who says that in the song of an Iowa specimen the beat occurred 36 times in 10 seconds at 61° F, and 6 times per second at 70° F.

DISCUSSION

Taxonomists have long been aware of the high degree of consistency in the calling songs of the different individuals of a given species of Orthoptera, and the noticeable differences which almost invariably occur between the songs of different species. New species have been detected and are still being detected by differences in their songs that are a great deal more obvious, even to the ear alone, than are their morphological peculiarities. The song relationships demonstrated here indicate that detailed song comparisons may also be of value in clarifying phylogenetic relationships. The songs of *carolinus*, *confusus*, and *melodius*, though strikingly different in many individual elements of rhythm, still contain similarities which indicate mutual relationship, and which set them apart from the song of *maculatus*, a species placed in another subgenus on the basis of morphological characters.

Comparison of the types of song differences existing among the four species and the frequency with which the species occur mixed together in the same colonies in the field, indicates that variations in certain rhythmical elements may be more closely correlated with ecological distribution than with phylogenetic relationship. Thus, the basic pulse rate in the song of *melodius* is more different from that in the song of *carolinus* than it is from those in the songs of the other two species. The basic pulse rate is the only rhythmical element in the song of *melodius*, and although *carolinus* is the closest known relative of *melodius*, it is also the only *Nemobius* species found together with it in the field, other than *socius* which has a completely different song. *N. confusus* and *maculatus*, species which frequently live together and belong in different subgenera, have basic pulse rates much closer to that in the song of *melodius* than does *carolinus*, and even closer to each other. However, the songs of these species contain an additional rhythmical element, the rate of delivery of pulse groups, which is superimposed on the basic pulse rate. In this character they differ greatly. If this type of correlation is generally true, it would seem to substantiate the view that certain interspecific song differences are behaviorally significant, and operate as species-isolating mechanisms.

Comparisons of the individual elements of rhythm in the song of *carolinus* with those in the songs of *maculatus* and *confusus* are more difficult because of the complicated nature of this song, and particularly because of the introduction of progressive changes in intensity and in the length of pulse groups. The trills of *confusus* are delivered at a rate near the rate of alternation of smooth trills with pulsating trills in the alternately pulsating trill of *carolinus*, but *confusus* has no song characteristic resembling the rate of delivery of pulse groups in the pulsating trill of *carolinus*. Likewise, though the rate of delivery of pulse groups in the song of *maculatus* is near that which occurs in the song of *carolinus*, *maculatus* has no song character corresponding to the rate of alternation of pulsating and smooth trills in the alternately pulsating song of *carolinus*.

REFERENCES

Alexander, R. D. 1956. A comparative study of sound production in insects, with special reference to the singing Orthoptera and Cicadidae of the eastern United States. xviii+529 pp., 180 fig. (Unpublished Ph.D. Dissertation, The Ohio State University).

———. 1957. Sound production and associated behavior in insects. Ohio Jour. Sci. 57: 101–113, 13 fig.

Borror, D. J. and **C. R. Reese.** 1953. The analysis of bird songs by means of a Vibralyzer. Wilson Bull. 65(4): 271–275, 7 fig.

Cantrall, I. J. 1943. Orthoptera and Dermaptera of the George Reserve, Michigan. Mich. Mus. Zool., Univ. Mich. Misc. Publ. 54: 1–182, 3 fig., 2 maps, 15 tab., 10 pl.

Fulton, B. B. 1930. A new species of *Nemobius* from North Carolina (Orthoptera: Gryllidae). Ent. News 41: 38–42, 1 fig.

———. 1931. A study of the genus *Nemobius* (Orthoptera: Gryllidae). Ann. Ent. Soc. Amer. 24: 205–237, 5 fig.

———. 1932. North Carolina's singing Orthoptera. Jour. Elisha Mitchell Sci. Soc. 47: 55–69.

———. 1933. Inheritance of song in hybrids of two subspecies of *Nemobius fasciatus* (Orthoptera). Ann. Ent. Soc. Amer. 26: 368–376, 1 fig.

———. 1952. Speciation in the field cricket. Evolution 6(3): 283–295, 4 fig.

———. 1956. The genus *Anaxipha* in the United States (Orthoptera; Gryllidae). Jour. Elisha Mitchell Sci. Soc. 72(2): 222–243, 23 fig.

Gabbutt, P. D. 1954. Notes on the mating behavior of *Nemobius sylvestris* (Bosc.) (Orth., Gryllidae). Brit. Jour. Animal Behavior 2(3): 84–88, 5 fig.

Lutz, F. E. and **W. R. Hicks.** 1930. An analysis by movietone of a cricket's chirp (*Gryllus assimilis*). Amer. Mus. Novit. No. 420: 1–14, 2 tab., 5 fig.

Pielemeier, W. H. 1946. Supersonic insects. Jour. Acoust. Soc. Amer. 17: 337–338.

———. 1946a. Seeing summer sounds. Sci. Month. 62: 450–452.

Pierce, G. W. 1948. The Songs of Insects; with related material on the production, propagation, detection, and measurement of sonic and supersonic vibrations. Cambridge, Mass., Harvard Univ. Press. vi+329 pp., 243 fig., 26 tab.

Richards, T. J. 1952. *Nemobius sylvestris* in S. E. Devon. Entomologist 85: 83–87; 108–111; 136–141; 161–166.

———. 1953. *Nemobius sylvestris* (F.) (Orthopt., Gryllidae): a correction and some further notes. Entomologist 86: 133–134.

Thomas, E. S. and **R. D. Alexander.** 1957. *Nemobius melodius*, a new species of cricket from Ohio. Ohio Jour. Sci. 57: 148–152.