

THE ROBUST CONEHEAD: TWO WIDESPREAD SIBLING
SPECIES (ORTHOPTERA: TETTIGONIIDAE:
NEOCONOCEPHALUS "ROBUSTUS")^{1, 2}

T. J. WALKER, J. J. WHITESSELL, AND R. D. ALEXANDER

*Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32601,
and Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104*

ABSTRACT

The coneheaded katydids formerly known as "*Neoconocephalus robustus*" belong to two species: *robustus* (Scudder) and *bivocatus* n. sp. The two are sympatric in northeastern and midwestern United States, but *robustus* extends southward into Florida and Texas and westward into New Mexico. Populations of *robustus* in the Central Valley of California are apparently disjunct from the New Mexico populations and may be a result of recent introduction. Differences in calling song, width of the stridulatory area, and length of ovipositor are the most useful characters for separating the two species.

INTRODUCTION

Although they are numerous and conspicuous, the coneheaded katydids discussed in this paper have puzzled taxonomists for more than 100 years. In 1862 S. H. Scudder described two species: *robustus* (specimens from Cape Cod, Massachusetts) and *crepitans* (specimens from Texas and Nebraska). The Massachusetts specimens were smaller and had a narrower sharper fastigium or "cone" than the Texas-Nebraska ones. In 1913 W. T. Davis reported both *robustus* and *crepitans* from New Jersey and noted (p. 178) that the two species differed not only in the bluntness of the fastigium but also in song: "In August, 1912, additional material [of *crepitans*] was collected and the song listened to with care. While it consisted of the same continuous whirr as in *robustus*, it was not nearly so ear-splitting."

¹Florida Agricultural Experiment Station Journal Series No. 4970.

²Manuscript received June 27, 1973.

Davis also identified two specimens from Virginia as *crepitans* and remarked that eastern specimens of *crepitans* average less robust than western ones.

In their 1915 revision of United States *Neoconocephalus*, Rehn and Hebard concluded that *robustus* and *crepitans* were the same species; however, they recognized two races: *robustus robustus* (northeastern United States, Massachusetts to New Jersey) and *robustus crepitans* (southern and western United States, New Jersey to Florida to Texas and Minnesota). These authors used length and bluntness of the fastigium and body size to characterize the two races and stated (p. 389): "The area of intergradation between typical *robustus* and *robustus crepitans* is very unusually narrow. Large collections of the insect made on the Atlantic coast show that the intergradation takes place in the vicinity of Ocean View, New Jersey, and on the Delaware River in the vicinity of Philadelphia."

No changes in nomenclature have occurred since 1915, but various workers have had difficulty fitting their observations into the classification proposed by Rehn and Hebard. Allard (1916) detected the same dichotomy in calling songs that Davis had. Allard wrote (p. 357): "The stridulations of the majority of individuals around Clarendon [Virginia] and Washington consist of a rather weak, continuous, snappy z-z-z-z-z-z. Occasionally, however, other individuals produce an entirely different note which is exceedingly loud, penetrating, and continuous, with a peculiar droning whirr, and may be heard for long distances. So different are these notes that the writer was convinced he had captured another species. During the summer of 1915, several individuals characterized by the stronger note were taken. Although it was first thought that those individuals characterized by the stronger note were generally larger and possibly came closer to *N. robustus robustus*, it was finally decided to refer all to the form *N. robustus crepitans*. The question is not solved, however, and needs further investigation. . . . Occasionally, stridulations somewhat intermediate between the two extremes may be heard." Blatchley (1920) reported both *robustus robustus* and *robustus crepitans* from Indiana and pointed out that the specimens of *r. robustus* agreed with Scudder's type and with the key and description of Rehn and Hebard. Hebard (1934) recognized both *r. robustus* and *r. crepitans* in Illinois and stated (p. 210): "It is becoming increasingly apparent that this insect [*r. robustus*] may be the response to a sand environment in this species and not the typical race (*robustus crepitans*). We do not yet feel justified, however, in indicating synonymy."

Our introduction to the *robustus* problem was similar to that described above for Davis (in New Jersey) and Allard (in Virginia). In 1956 Alexander noted two contrasting songs for "*robustus*" in Hocking County, Ohio: an ear-splitting whine and a loud buzz. He collected a series of "whiners" and a series of "buzzers," but some specimens among the buzzers could not be distinguished morphologically from whiners. He told Walker of the problem and Walker eventually told Whitesell (in 1968). The three of us have worked to accumulate specimens, tape recordings, and listening records of buzzers and whiners. In 1970 Walker, with assistance from Whitesell, made high-speed sound-synchronized movies of the wing movements of stridulating buzzers and whiners. The movements were so strikingly different that we made a new effort to resolve the taxonomic status of individuals making the two different calling songs.

In this paper we will show that two species of "*robustus*" exist, and that they can be distinguished by calling song (as well as by certain structural features). However, the calling song differences are not entirely the same as those originally noted by Davis and Allard (nor, for that matter, by us).

EVIDENCE FOR TWO SPECIES

Song

Oscillographic (fig. 1) and audiospectrographic analyses of "*robustus*" calling songs have revealed a dichotomy that only partially correlates to the buzzes vs.

whines distinguished by the human ear. This dichotomy is in the spacing of the pulses (major bursts of sound) within the calling song. In the species here named *bivocatus*, calling songs are buzzes, and consecutive intervals between pulses are unequal, whereas alternate ones are equal (fig. 1A). In the species that retains the name *robustus*, all pulse intervals are approximately the same (fig. 1B-E). Most songs of *robustus* are intense and whiney (fig. 1B, C); however, *robustus*

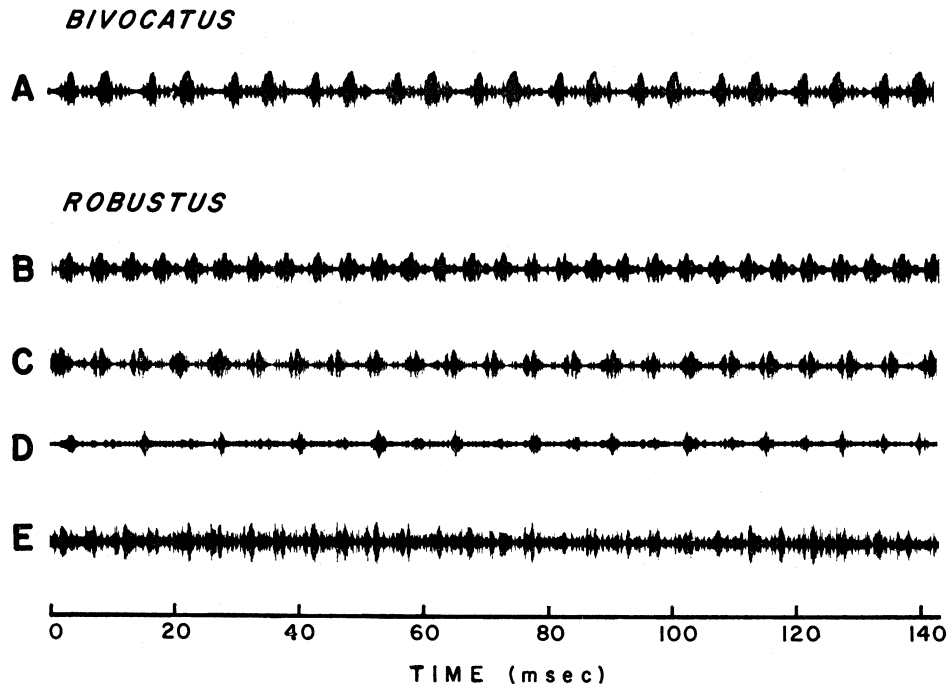


FIGURE 1. Oscillograms of calling songs. A. *N. bivocatus*, 24°C, Cecil Co., Md. (Note that alternate intervals are similar while adjacent intervals are different.) B-E. *N. robustus*. B-C. Usual pattern; associated with whinelike quality; two individuals, 23°C, Lafayette Co., Mo. D. Same individual and occasion as C, but at a time when song had a buzzy quality similar to that of *bivocatus*. (Note that alternate major sounds are similar while adjacent major sounds are different.) E. Song with splattery quality, 29°C, Barnstable Co., Mass.

songs in which consecutive pulses are not similar (fig. 1D, E) have a buzzy quality that makes them difficult to distinguish by ear from those of *bivocatus*. In other words "whiners" are always *robustus*, but "buzzers" may be either *bivocatus* or *robustus*. Electronic analysis can be used to distinguish buzzers that produce pulses in pairs (*bivocatus*) from other buzzers (*robustus*).

The relation between phonatome rate and temperature for the two species is illustrated in figures 2 and 3. A phonatome is an acoustical unit corresponding to one complete cycle of wing movement (Walker and Dew, 1972). In most species of crickets and kaydids a plot of phonatome rate vs. ambient temperature approximates a straight line, with a coefficient of determination (r^2) of the regression generally 0.9 or higher (e.g., Walker, 1962; Walker, 1974a). The scatter of the points about the regression lines of *robustus* ($r^2=0.52$) and *bivocatus* ($r^2=0.72$) is greater than for any comparable data yet published. One factor that must contribute to the scatter in *robustus* is that the thoracic temperature of this species is as much as 12°C above ambient during singing and changes during the course of the song (Heath and Josephson, 1970).

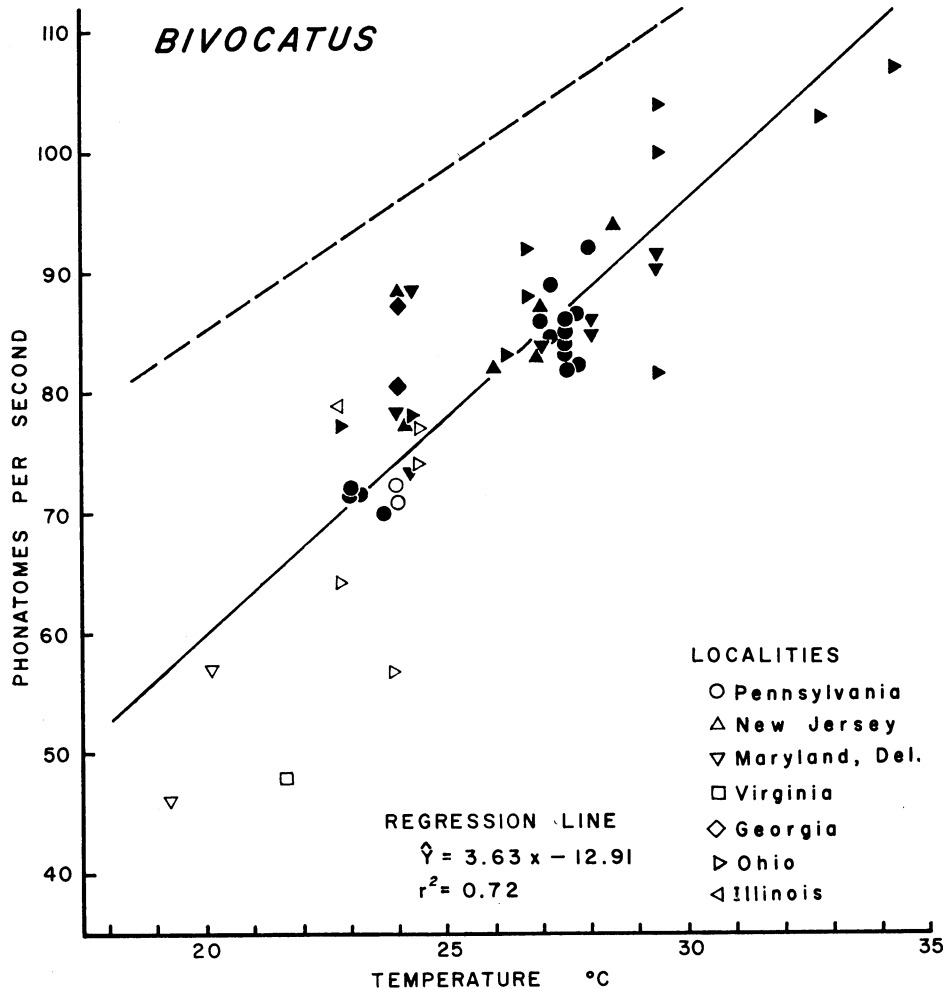


FIGURE 2. Effect of temperature on the calling song of *N. bivocatus*. Each point represents a separate tape recording and is calculated from the time required for approximately 50 phonatomes. Solid symbols indicate laboratory recordings of caged individuals; open symbols indicate field recordings. The solid line is the regression line for *bivocatus* (phonatome rate on °C), and the dotted line is the regression line for *robustus* (phonatome rate $\div 2$ on °C; *robustus* has a single acoustically effective wing closure during each phonatome while *bivocatus* has two).

Wing Movements

Walker (1974b) reported on high speed sound-synchronized photography of the stridulatory wing movements of *robustus* and *bivocatus*. The pulses are made during wing closures. Because the first of each pair of pulses in *bivocatus* is produced by a partial closure and the second is produced by a full closure, the wing movement becomes repetitive only after a pair of wing closures. Therefore the phonatome has two pulses. In *robustus*, on the other hand, the wing movement becomes repetitive after a single closure, and the phonatome has a single pulse.

Morphology

The size and shape of the fastigium—used by Rehn and Hebard and others to separate "*robustus*" and "*crepitans*"—are not reliable means of distinguishing

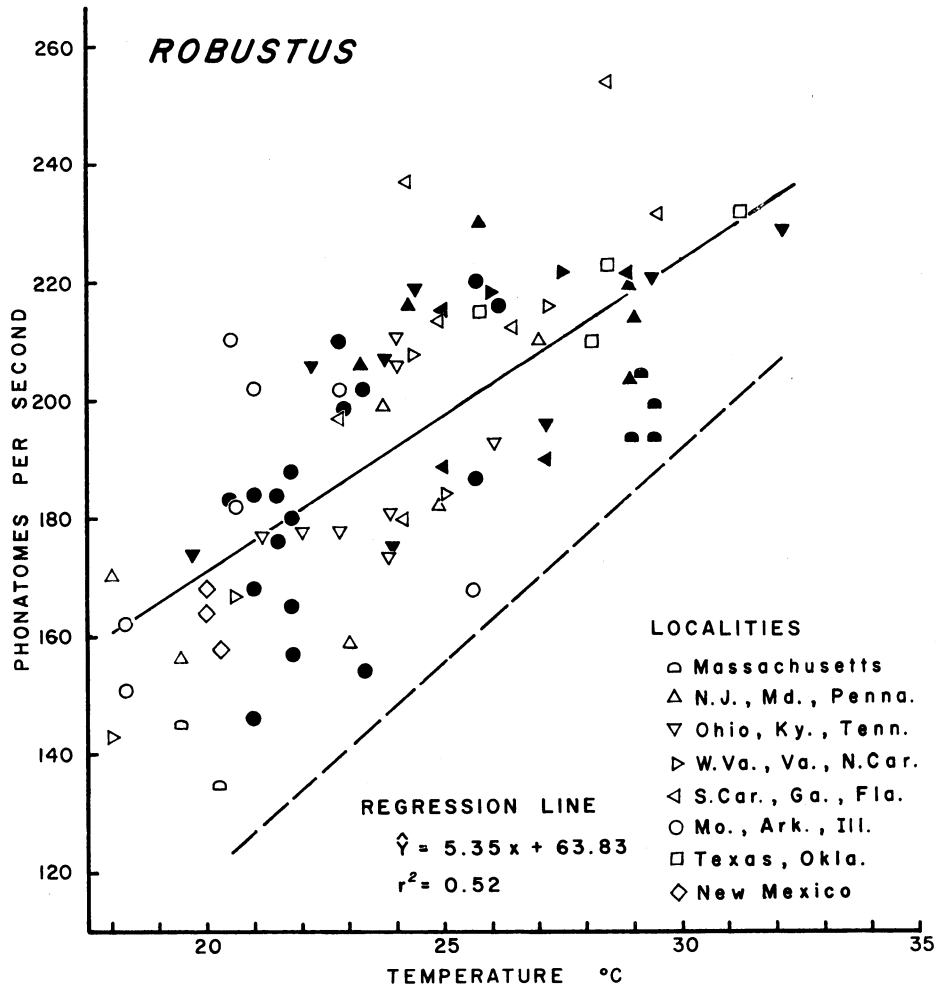


FIGURE 3. Effect of temperature on the calling song of *N. robustus*. Each point represents a separate tape recording and is based on the time required for approximately 100 phonatomes. Solid symbols indicate laboratory recordings of caged individuals; open symbols indicate field recordings. The solid line is the regression line for *robustus* (phonatome rate on °C), and the dotted line is the regression line for *bivocatus* (phonatomes $\times 2$ on °C).

bivocatus and *robustus* (figs. 7-13). The morphological identifying feature we found most useful was the width of the stridulatory field (fig. 6, table 1). Most specimens of *bivocatus* (35 or 37) had widths of less than 4.9 mm, whereas most of *robustus* (67 of 69) had widths greater than 4.9 mm. Specimens of *robustus* from Massachusetts averaged smaller in all respects (including width of stridulatory field, table 1) than those from farther south.

Neither the number of teeth in the stridulatory file nor the length of the stridulatory file proved useful as identifying characters. For 5 males of *bivocatus* the mean number of teeth was 84 (range 80-92) and the mean length was 2.5 mm (range 2.4-2.6). For 10 males of *robustus* the mean number of teeth was 85 (78-96) and the mean length was 2.7 mm (range 2.5-3.0).

Females of *bivocatus* have absolutely and proportionally longer ovipositors than *robustus*. Two females of *bivocatus* (1 was from a mating pair) had ovipositors 38 and 39 mm long and 1.3× and 1.4× the length of the hind femur. Thirty females of *robustus* (including 1 from a mating pair and 4 from well beyond the range of *bivocatus*) had ovipositors 26–37 mm long and 1.0×–1.1× the length of the hind femur.

TABLE I
Width of stridulatory area in males of *N. robustus* and *bivocatus*

Species	No.	Range (mm)	$\bar{X} \pm SD$
<i>N. robustus</i>			
Massachusetts	10	4.5–5.3	5.0±0.2
16 other states	59	4.8–6.0	5.5±0.3
all states	69	4.5–6.0	5.4±0.3
<i>N. bivocatus</i>			
5 states	37	4.5–5.0	4.7±0.1

KEY

The following couplet can be added to the *Neoconocephalus* keys of Rehn and Hebard (1915) or Blatchley (1920) in each place that "*robustus*" or "*crepitans*" is identified:

- X. Calling song with long and short intervals alternated (fig. 1A), never whinelike; width of stridulatory area (as measured in fig. 6) less than 4.9 mm; length of ovipositor more than 1.2× length of hind femur; range as in figure 4. *bivocatus*
- XX. Calling song with consecutive intervals approximately equal (figs. 1B–D), usually whinelike; width of stridulatory area greater than 4.9 mm; length of ovipositor less than 1.2× length of hind femur; range as in figure 5. *robustus*

NOMENCLATURE AND DESCRIPTION OF NEW SPECIES

Neoconocephalus robustus (Scudder) Robust Conehead

Synonymy

Conocephalus robustus Scudder, 1862: 449.

Conocephalus crepitans Scudder, 1862: 450.

Neoconocephalus robustus robustus (Scudder), Rehn and Hebard 1915: 387.

Neoconocephalus robustus crepitans (Scudder), Rehn and Hebard 1915: 391.

Dr. H. E. Evans, Museum of Comparative Zoology, Harvard University, kindly sent three type specimens each of *Conocephalus robustus* Scudder and *C. crepitans* Scudder. All specimens belonged to the species here called *robustus*. Rehn and Hebard (1915) had previously designated lectotypes, and for *C. robustus* they had picked the least robust syntype—width of stridulatory area 4.7 mm as compared with 5.2 and 5.3 mm for the other two syntypes. The proportions of the lectotype, however, marked it as the species here called *robustus* rather than the species here named *bivocatus*. Furthermore, its place of collection and its fastigial shape (fig. 9) were outside the ranges known for *bivocatus* (figs. 4, 7, 8).

Neoconocephalus bivocatus n. sp.

False Robust Conehead
(figs. 1, 2, 4, 7, 8)

N. bivocatus differs from *robustus* by the characters listed in the key above. The name *bivocatus* refers to the two-pulsed phonatome.

Holotype: ♂, Maryland Rt. 7, 1.2 mi N of U.S. 40, Cecil Co., Maryland, 15 Aug. 1967, TJJW; Univ. Fla. Tape 189–6; deposited in Univ. Mich. Mus. Zool. General color green; narrow transverse black mark at apex of fastigium. Fastigium as in fig. 7. Stridulatory file 2.37 mm with 92 teeth.

Allotype: ♀, Kennett Square, Chester Co., Pennsylvania, 3 Aug. 1969, JJW: one of mating pair; deposited in Univ. Mich. Mus. Zool. General color green. Fastigium unmarked, shape as in fig. 8. Terminal 30 mm of ovipositor straight.

Measurements of holotype and allotype (mm): Length of body, ♂ 33, ♀ 37; pronotal disc (length×caudal width), ♂ 8.3×5.4, ♀ 8.5×5.4; length of tegmen, ♂ 42, ♀ 53; length of hind femur, ♂ 23, ♀ 28; length of ovipositor, 38.

Paratypes: 77 ♂, Fla. St. Coll. Arthrop. (FSCA); 37 ♂, 1 ♀, Univ. Mich. Mus. Zool. (UMMZ). NEW JERSEY: Cape May Co., 15 ♂, 28 July–22 Aug. 1937, 1 ♀, 1 Sept. 1937, Henry Fox (UMMZ), 6 ♂, 30 July 1969, 25 July 1970, JJW (FSCA; incl. Univ. Florida (UF) Tapes JJW 127, 128, 130, 281, 294); Ocean Co., 1 ♂, 17 Aug. 1967, TJW (FSCA; UF Tape 189–8). DELAWARE: New Castle Co., 1 ♂, 24 Aug. 1968, JJW (FSCA). PENNSYLVANIA: Delaware Co., 14 ♂, 25 Aug. 1968, 23 July 1970, JJW (FSCA; incl. UF Tapes JJW 52, 53, 273–275, 283, 291); Chester Co., 16 ♂, 3 Aug. 1969, 24 July 1970, JJW (FSCA; incl. UF Tapes JJW 132–135, 276, 278, 279, 282, 288). MARYLAND: Cecil Co., 9 ♂, same data as holotype (FSCA; incl. UF Tapes 189–4, 7, 8); Prince Georges Co., 2 ♂, 9 Aug. 1969, JJW (FSCA); Montgomery Co., 5 ♂, 10 Aug. 1969, JJW (FSCA). VIRGINIA: Falls Church, 28 July, Banks Colln. (UMMZ). WEST VIRGINIA: Greenbrier Co., 1 ♂, 1 Sept. 1972, TJW (FSCA, UF Tape 72–41). GEORGIA: Rabun Co., 3 ♂, 15 Aug. 1970, TJW (FSCA; incl. UF Tapes 189–17, 18). TENNESSEE: Fentress Co., 1 ♂, 20 Aug. 1924, T. H. Hubbell (UMMZ). KENTUCKY: Barren Co., 1 ♂, 24 Aug. 1972, TJW (FSCA). OHIO: Hocking Co., 1 ♂, 11 Sept. 1932, R. M. Bailey; 11 ♂, 8 and 13 Aug. 1956, RDA (UMMZ); 2 ♂, 13 Aug. 1956, TJW (FSCA; UF Tapes 189–1, 2); Washington Co., 17 ♂, 20–21 Aug. 1967, 18 Aug. 1970, 28–29 Aug. 1972, TJW (FSCA; incl. UF Tapes 189–9, 10). ILLINOIS: Pope Co., tape only, 7 Aug. 1967 (UF Tape 189–3). KANSAS: Franklin Co., 1 ♂, 2 Aug. 1927, Wesley Clinton (UMMZ). OKLAHOMA: Rogers Co., 7 ♂, 23 July 1926, T. H. Hubbell (UMMZ).

Color dimorphism: Of 114 males, 86 are green and 28 are brown; of 2 females, 1 is green and the other is brown. The only series that is predominantly brown (10 of 15) is from Ocean View, Cape May County, New Jersey, collected by Henry Fox.

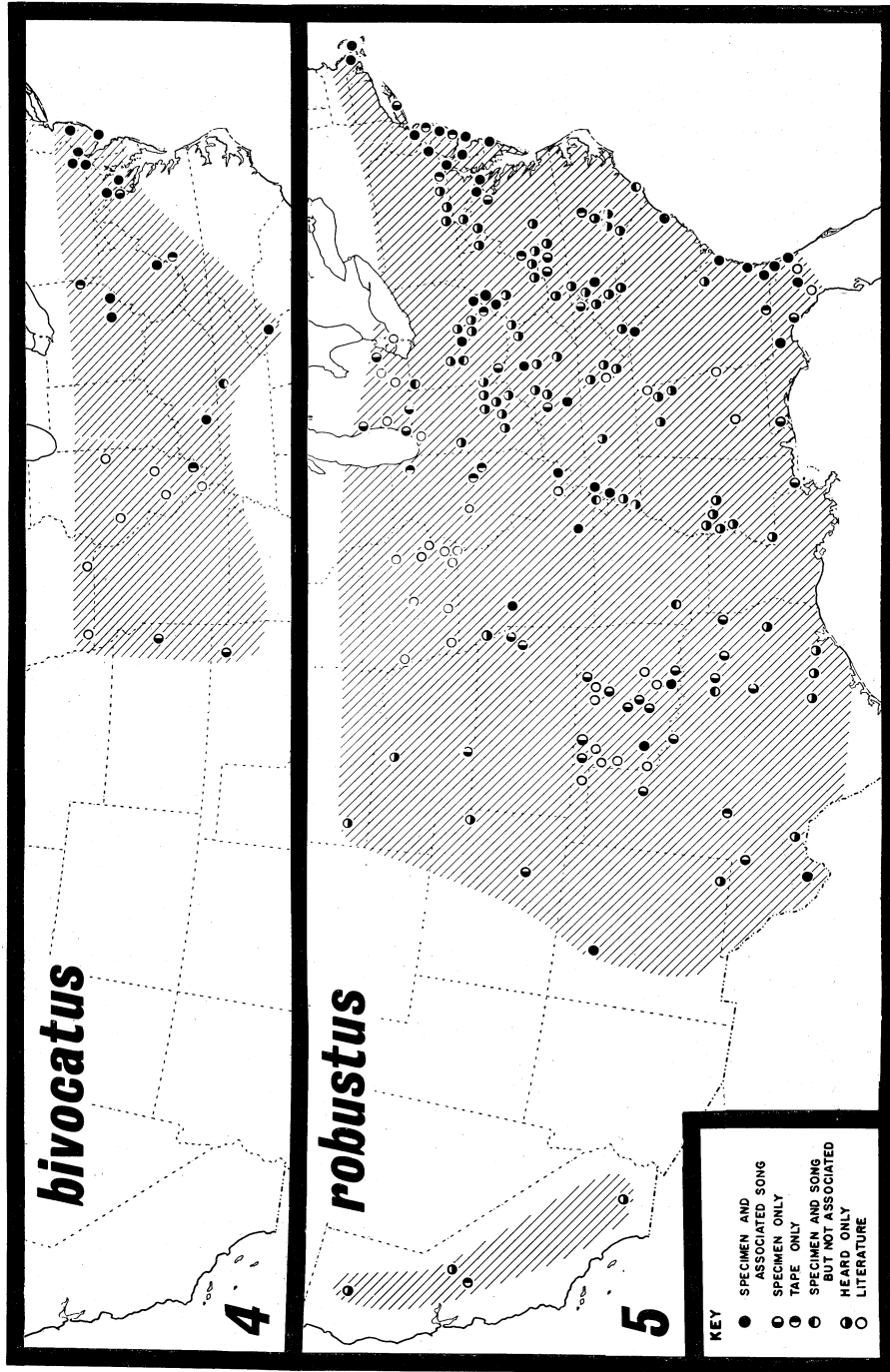
ECOLOGY

Geographical Distribution

Figures 4 and 5 show the known and predicted distributions of *bivocatus* and *robustus*. The populations of *robustus* in California are apparently disjunct from the eastern populations. All California records are by Alexander in 1963. We do not know how long *robustus* has been in California. Its presence may be the result of a recent introduction. Peripheral records are documented as follows: *N. bivocatus* (records other than paratypes)—IOWA, Davis Co. and Page Co. (Froeschner 1954: 283); OHIO, Jefferson Co. (UMMZ Tape A46–1). *N. robustus*—CALIFORNIA, Riverside Co., ca. 14 mi S? from Indio, 19 July 1963 (RDA field notes); Shasta Co., near Igo, 11–14 July 1963 (*ibid.*); Tuolumne Co., Chinese Corner, 23–28 Aug. 1963 (*ibid.*); Merced Co., near Los Banos, 16 July 1963 (UMMZ Tape); NEW MEXICO, Sandoval Co., near Corrales, 22 Aug. 1968 (UF Tapes 195–6, 7, 8; FSCA); SOUTH DAKOTA, Pennington Co., Wall, 5 July 1963 (RDA field notes); MICHIGAN, Muskegon Co., Muskegon St. Pk., 17, 18 Aug. 1935 (UMMZ); Oakland Co., Milford, 14 Sept. 1946 (UMMZ); MASSACHUSETTS, Plymouth Co., 30 Aug. 1970 (UF Tapes JJW 324, 330, 321; FSCA); Barnstable Co. (type locality; UF Tapes JJW 326, 328, 332; FSCA); FLORIDA, St. Johns Co., 19 June 1965 (FSCA); Levy Co., 14 Aug. 1905 (Rehn and Hebard 1907: 304); TEXAS, Harris Co., 18 June 1962 (RDA field notes); Brewster Co., near Rio Grande Village, Big Bend Nat. Pk., 13 and 16 Aug. 1968 (UF Tape 195–5; FSCA).

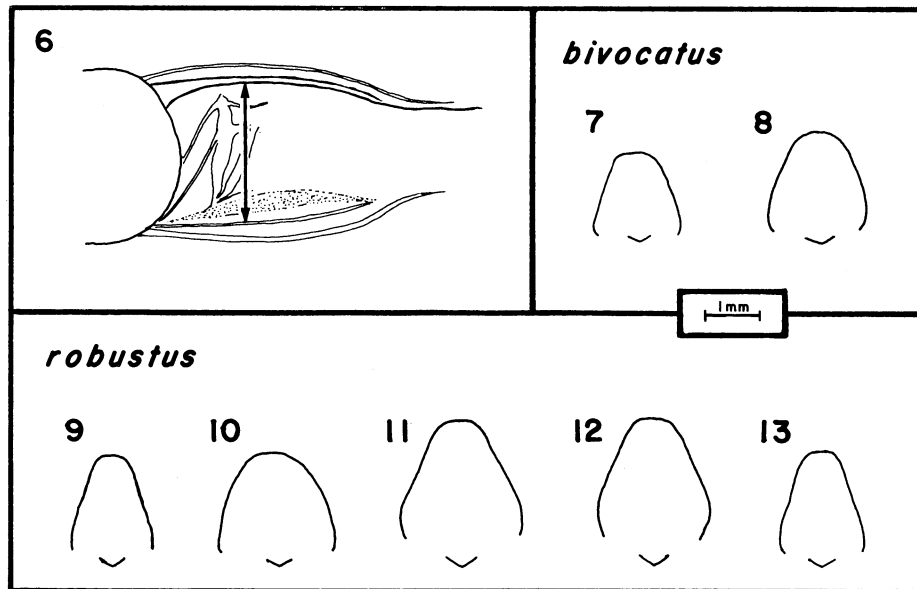
Seasonal Life Cycles

N. bivocatus and *robustus* are univoltine throughout their ranges and overwinter in the egg stage. In areas where both occur their mating seasons broadly overlap,



FIGURES 4-5. Distribution of *N. bivocatus* and *N. robustus*. Circles show county records. The predicted distribution is shaded. Peripheral records are substantiated in the text.

but *bivocatus* peak abundance precedes that of *robustus* by at least 2 weeks (JJW, near Philadelphia; TJW, Washington Co., Ohio). The peaks of abundance for *robustus* in southern demes are only a few weeks earlier than for northern demes (e.g., early August in Alachua Co., Fla.; compared to middle or late August near Philadelphia). The earliest and latest records for adult male *robustus* are 16 June (1956, Pike Co., Ark., TJW, FSCA) and 6–12 Oct. (1935, Franklin Co., Kans., Wesley Clinton, UMMZ); for *bivocatus*, 23 July and 1 Sept. (see list of paratypes for specifics).



FIGURES 6-13. 6. Stridulatory area of *N. robustus* with arrow showing how width is measured from the median line of a yellow ridge (below) to the edge of the left tegmen (above). The point along the yellow ridge is selected to give the maximum measurement, but the width measured from this point is the shortest distance to the edge of the tegmen. 7-13. Ventral views of fastigia. Scale indicated at center right. 7-8. *N. bivocatus*. 7. Holotype. 8. Allotype. 9-13. *N. robustus*. 9. Lectotype of *robustus* (♂, Cape Code, Mass.). 10. Lectotype of *crepitans* (♀, Texas). 11. Female paralectotype of *crepitans*; Nebraska. 12. Male; Cape May Co., N. J. 13. Male; Middlesex Co., N. J.

Habitat

Males of *bivocatus* and *robustus* often sing in the same habitats at the same time. However, *bivocatus* males generally sing from lower less exuberant vegetation, whereas *robustus* males are most abundant in tall rank vegetation. Males of *bivocatus* usually sing from within the vegetation and usually dive downward and run laterally when disturbed. Males of *robustus* characteristically sing on the periphery (often high) of the vegetation and generally fly when disturbed. A typical situation occurred at the type locality of *bivocatus*: *bivocatus* was numerous near the ground in a rundown weedy pasture; *robustus* was singing from 2 m up in a nearby well-fertilized corn field. In Delaware County, Pennsylvania, JJW never heard *robustus* in the hilly well-drained piedmont region but only in the lower coastal plain—mostly in tall grass, such as *Phragmites communis*, near marshes. Rehn and Hebard must have observed the same transition (see quote in the second paragraph of this paper). Along the Atlantic Coast *robustus*, but not *bivocatus*, occurs at the edges of salt marshes and in the wet areas back of dunes.

For example, on the night of 17 Aug. 1967, as TJW drove west on New Jersey Rt. 526, he heard many *robustus* near the coast, but not until the topography changed one mile east of Jackson Mills were any *bivocatus* heard. Similarly, on the nights of 30 July 1969 and 25 July 1970, as JJW drove west on New Jersey Rt. 47, he heard many *robustus* in *Phragmites communis* near the salt marshes, but not until the marshes were replaced by weedy fields near Rio Grande did he hear *bivocatus* as well.

Males, and presumably females, of *robustus* are strong fliers and they should be able to reoccupy wet places in the western prairies and deserts after drought years. For instance, a male was captured in an isolated water seepage area in the Chihuahuan desert, Big Bend National Park, Texas, about 10 miles from the Rio Grande River.

ACKNOWLEDGMENTS

We thank Dr. H. E. Evans for loaning the types of *robustus* and *crepitans*. We thank also the National Science Foundation for support during much of the field work (GB 20749 and others to TJW).

REFERENCES CITED

- Allard, H. A. 1916. Some musical Orthoptera at Clarendon, Virginia. *Can. Entomol.* 48: 356-358.
- Blatchley, W. S. 1920. Orthoptera of northeastern America. Nature Publ. Co., Indianapolis. 784 p.
- Davis, W. T. 1913. Two additions to the list of New Jersey coneheaded grasshoppers. *N. Y. Entomol. Soc.* 21(3): 177-178.
- Heath, J. E., and R. K. Josephson. 1970. Body temperature and signing in the katydid, *Neoconocephalus robustus* (Orthoptera, Tettigoniidae). *Biol. Bull.* 138: 272-285.
- Hebard, M. 1934. The Dermaptera and Orthoptera of Illinois. *Bull. Ill. Nat. Hist. Surv.* 20(3): 125-279.
- Rehn, J. A. G., and M. Hebard. 1915. Studies of American Tettigoniidae (Orthoptera): III. A synopsis of the species of the genus *Neoconocephalus* found in North America north of Mexico. *Trans. Amer. Entomol. Soc.* 40: 365-413.
- Scudder, S. H. 1862. Materials for a monograph of the North American Orthoptera, including a catalogue of the known New England species. *J. Boston Soc. Nat. Hist.* 7: 409-480.
- Walker, T. J. 1962. Factors responsible for intraspecific variation in the calling songs of crickets. *Evolution* 16(4): 407-428.
- 1974a. Effects of temperature on wingstroke rates during calling in meadow katydids (Orthoptera: Tettigoniidae: *Orchelimum*). *J. Insect Physiol.* 20: tendered.
- 1974b. Wing movements during stridulation in eight species of coneheaded katydids (Orthoptera: Tettigoniidae: *Neoconocephalus*). *J. Insect Physiol.* 20: tendered.
- Walker, T. J., and D. Dew. 1972. Wing movements of calling katydids: fiddling finesse. *Science* 178: 174-176.