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COVER

Stridulatory file (scanning electron micrograph) of Uhler's katydid. The file is on the underside of the left forewing. Here the forewing is ventral surface up; the 134 file teeth form a 2.8-millimeter row curving posteriorly from lower left to upper center. See page 174. [Insect Attractants, Behavior and Basic Biology Research Laboratory, U.S. Department of Agriculture, Gainesville, Florida; courtesy of P. S. Callahan and T. Carlysle]

Abstract. *Stridulating Uhler's katydids produce the most complex song known for insects. Series of four types of sounds are made in stereotyped sequence. Sound-synchronized high-speed photography reveals that each type of sound is produced by a distinctively different wing-movement cycle. The most complex of these cycles includes a two-step closure and a nearly silent close-open movement.*

The species-specific calling songs of male crickets and katydids (Orthoptera: Gryllidae and Tettigoniidae) have been used in studies of systematics (*1*), communication (*2*), biophysics (*3*), and neurophysiology (*4*). Such sounds are made by the scraper of one fore wing stroking the file of the other. Most species use only one type of wing-movement cycle during calling, and hence produce only a single "phonatome," that is, a single major acoustical unit corresponding to a cycle of wing movement (*5*). Their songs, then, are sequences of a single phonatome. On the other hand, some species use two or more stroking techniques during calling, and hence their songs include sequences of two or more phonatomes.

Although earlier workers have used photography to determine the relation between wing movements and the sounds produced during calling, in each case the sounds investigated suggested repetitions of a single phonatome, and a single type of wing-movement cycle was indeed found (*6, 7*). This report describes the relation between wing movements and sounds in Uhler's katydid, the only insect known to produce four phonatomes (*8*).

These katydids produce sequences of each of their four phonatomes in a stereotyped pattern lasting 8 seconds or longer. In the species studied here the calling song (Fig. 1A) begins with a sequence of 50 to 80 phonatomes of one type (hereafter designated type I). Immediately following is a sequence of 7 to 12 type II phonatomes and a sequence of 4 to 7 type III phonatomes. After a brief pause the katydid produces another sequence of 4 to 7 type III phonatomes. It may produce additional sequences of 4 to 7 type III phonatomes, but eventually it interposes one

Table 1. Comparison of four types of phonatomes produced by Uhler's katydids from Washington County, Ohio.

Phonatome type	Usual number of phonatomes in sequence	Approximate duration at 25°C (msec)	Approximate repetition rate at 25°C (sec^{-1})	Maximum sound intensity (relative)*	Amplitude of wing opening (relative)	Special features
I	50–80	70	14	0–20	50	Intensity increases during sequence; short pause during closing
II	7 12	110	9	22–26	100	Long pause during closing; nearly silent close-open
III	4–7†	45	23	28–0	100–65	Intensity decreases during sequence; wing-opening amplitude decreases during sequence
IV	3–14	20	2	18–22	20	Wing movements slight

*Based on decibel readings from a tape recorder volume-unit meter (indicates the intensity of the volume of the signal during the tape recording); agrees with subjective impression of intensity. Frequencies above 20 khz were excluded by the microphone. † More than one sequence of 4 to 7 type III phonatomes may be produced without intervening sounds.

or more sequences of 3 to 14 type IV phonatomes. The katydid pauses before beginning a new bout of calling with 50 to 80 type I phonatomes. In the sequences of type I phonatomes the intensity gradually increases, and in the sequences of type III phonatomes the intensity rapidly decreases (9).

By a previously described technique of high-speed sound-synchronized photography (7), we filmed five calling males at 1000 to 2000 frames per second. We simultaneously tape-recorded the calls. Frame-by-frame measurement of wing position and filmed oscilloscopic trace revealed that the four phonatomes were produced by the wing-stroking movements illustrated in Fig. 1, B–E, and described below and in Table 1.

The type I phonatome (Fig. 1, B and C; two individuals filmed; $n = 23$ wing-movement cycles analyzed) is produced by a rapid opening of the fore wings followed by a slow closing. The closing usually has a hesitation near the end that produces a break in the sound longer than that occurring at either reversal of the direction of wing movement. The slow increase in intensity during a sequence of type I phonatomes is apparently produced by increased force of contact and not by change in the amplitude of wing movement.

During the type II phonatome (Fig. 1, C and D; three individuals; $n = 18$) the wings are opened more widely and closed more completely than in the type I phonatomes. The closing movements are faster, and the pause between the first and second portions of closing lasts longer than the closing movements themselves. The sound produced by the second portion of closing begins abruptly, suggesting release of energy mechanically stored during the pause. Opening immediately follows the second portion of closing and produces a burst of sound similar to that of the corresponding movement in type I phonatomes. After this acoustically effective opening, the wings partially close and then open more fully. This close-open movement is nearly silent.

The type III phonatome (Fig. 1, C and D; four individuals; $n = 22$) involves a rapid closing followed by a rapid opening. The extent of opening decreases during a sequence, yet the duration of closing increases. These two changes have the effect of maintaining a fairly constant period for successive type III phonatomes except for the terminal one or two.

The type IV phonatome (Fig. 1E; one individual; $n = 5$) is a two-pulse, tick-like sound made by scarcely perceptible

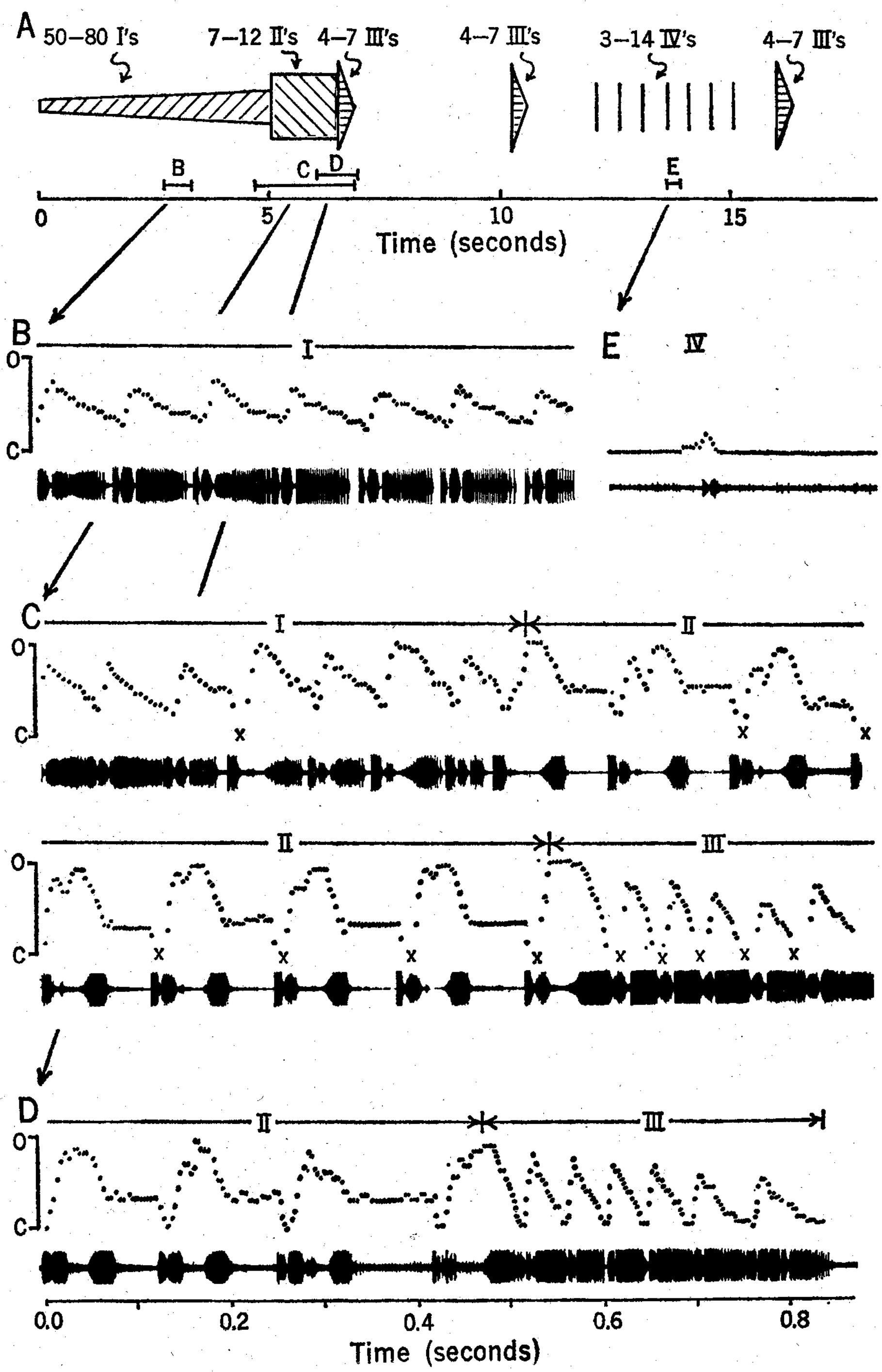

Fig. 1. Calling song and corresponding wing movements of Uhler's katydid. (A) Usual pattern of phonatome production during calling song (see text). The vertical dimension indicates intensity. Horizontal lines just above the time scale indicate sources of details B–E. (B–E) Wing movements (dots) and corresponding oscillograms. Wing movement is shown by the extent of wing separation measured during every fifth frame of film (on the vertical scale at the left *O*, fully open; *C*, fully closed). Roman numerals above each graph indicate the type of phonatome being produced. Each wing-movement graph is from a different film, and only (B) and (D) are of the same individual. The amplitudes of the various oscillograms are not to the same scale. Frequencies below 10 khz [below 20 khz for (E)] were filtered out before the oscillograph was made. In (E) the camera noise is still conspicuous. (B) Graph of 6½ type I phonatomes; the briefest spikes probably correspond to the striking of individual file teeth. (C) (Graph continues from one line to the next) Graph of 7 type I phonatomes (final 5 foretelling transition to type II), 7 type II phonatomes, and 6 type III phonatomes (×'s indicate frames for which the extent of closure could not be measured). (D) Graph of 3 type II, and 7 type III phonatomes. (E) Graph of 1 type IV phonatome.

wing movements. From our film we could not positively associate a particular wing movement with either of the two pulses. Twenty independent analyses of the five filmed type IV phonatomes showed these apparent movements during the first pulse: opening, $n = 7$; closing, $n = 1$; no movement, $n = 12$. Corresponding figures for apparent movements during the second pulse were as follows: opening, $n = 2$; closing, $n = 14$; no movement, $n = 4$. The first pulse is probably produced by an opening movement and the second by a closing.

The transitions from type I to type II and from type II to type III phonatomes are distinctive. The sequence of type I phonatomes ends with several that are variable (Fig. 1C; two films; two individuals). The amplitude of wing movement is greater (suggesting type II), the period becomes shorter (suggesting type III), and sometimes opening or a portion of closing is silent. Sometimes a group of such erratic type I phonatomes is followed by a short sequence of regular ones, that gives way again to erratic type I and then to type II phonatomes. Perhaps the katydid successfully shifts to type II phonatomes after an initial failure. The transition from type II to type III phonatomes is sudden (Fig. 1, C and D; four films; four individuals). The final type II phonatome has a slightly prolonged hold during closing, and the initial type III phonatome has a closing sound that begins gradually (as in type II phonatomes).

The complexity of wing movements in this species far exceeds any previously described. Those working with simple movements in one- or two-phonatome species (*2–4*) should note the challenges that remain. Systematists should note that wing-movement cycles provide an important new clue to homology and analogy among signals (*10*). Those taxonomists who have assumed that the distinctive features of the calling song can be deduced from features of the stridulatory apparatus (*11*) should note that four phonatomes come from a single apparatus and that the variety of distinctive calling songs one such apparatus might produce by changes in the sequence and timing of the four phonatomes would easily exceed the number of species of katydids.

The structure of the stridulatory file of Uhler's katydid merits comment. For instance, one might expect that the file would show some specialization facilitating the two-step closures of type I and type II phonatomes. In fact, certain species of Phaneropterinae (the subfamily including Uhler's katydid) have the most complex files known: some files have sharp bends, and others have sudden transitions in the structure and spacing of the teeth (*12*). However, the file of Uhler's katydid is remarkably ordinary—a row of nearly uniform teeth gently curving at either end (see cover). The calling songs of phaneropterines with complex files are unknown.

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References and Notes

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2. See, for example: B. Dumortier, *Ann. Epiphyt. Paris* **14**, 5 (1963); J. D. Spooner, *Anim. Behav.* **16**, 197 (1968); R. D. Alexander, in *Animal Communication*, T. A. Sebeok, Ed. (Indiana Univ. Press, Bloomington, 1968), p. 167.
3. See, for example: H. C. Bennet-Clark, *J. Exp. Biol.* **52**, 619 (1970); *Nature* **234**, 255 (1971); W. J. Bailey and W. B. Broughton, *J. Exp. Biol.* **52**, 507 (1970); G. K. Morris, *Can. Entomol.* **102**, 363 (1970).
4. See, for example: W. Kutsch and F. Huber, *Z. Vergl. Physiol.* **67**, 140 (1970); D. R. Bentley and R. R. Hoy, *Science* **170**, 1409 (1970); D. R. Bentley, *ibid.* **174**, 1139 (1971); D. Möss, *Z. Vergl. Physiol.* **73**, 53 (1971); R. K. Josephson and R. C. Halverson, *Biol. Bull.* **141**, 411 (1971).
5. Y. Leroy [*Signaux Acoustiques, Comportement et Systématique de Quelques Espèces de Gryllides* (*Orthoptères, Ensifères*) (Fanlac, Périgneux, France, 1966), p. 16] uses phonatome in this sense. The terms "chirp" and "syllable" have also been used but have other widely recognized acoustical meanings.
6. G. W. Pierce, *The Songs of Insects* (Harvard Univ. Press, Cambridge, Mass., 1948); F. Pasquinelly and M.-C. Busnel, in *Colloque sur l'Acoustique des Orthoptères*, R.-G. Busnel, Ed. (Institut National de Recherche Agronomique, Paris, 1954), p. 146; E. S. Thomas and R. D. Alexander, *Occas. Pap. Mus. Zool. Univ. Mich. 626* (1962), p. 26; W. J. Davis, *Anim. Behav.* **16**, 72 (1968).
7. T. J. Walker, J. F. Brandt, D. Dew, *Ann. Entomol. Soc. Amer.* **63**, 910 (1970).
8. Uhler's katydid constitutes a complex of at least five sibling species. All are now known as *Amblycorpha uhleri* Stal and all have calling songs with four phonatomes. The specimens photographed in this study were from Washington County, Ohio, where only one of the siblings occurs.
9. The song of this species of Uhler's katydid is more fully illustrated by R. D. Alexander, in *Animal Sound and Communication*, W. E. Lanyon and W. N. Tavolga, Eds. (American Institute of Biological Sciences, Washington, D.C., 1960), p. 72. The adaptive significance of the four phonatomes is not known, but three of them may be homologous to the three of the Texas bush katydid, for which J. D. Spooner has demonstrated distinctive functions [*Anim. Behav.* **12**, 235 (1964)].
10. Distinctive wing-movement cycles reveal distinctive neuromuscular mechanisms that would otherwise remain hidden to the systematist. These underlying mechanisms should be less subject to rapid evolutionary change than the sound patterns themselves, since only the sound patterns function directly in reproductive isolation.
11. W. W. Moss, D. A. Nickle, M. G. Emsley, *Notulae Natur. Philadelphia* **432**, 8 (1970).
12. Y. Leroy, *C. R. H. Acad. Sci. Paris* **270**, 96 (1970); M. G. Emsley and D. A. Nickle, *Proc. Acad. Natur. Sci. Philadelphia* **12**, 25 (1969).
13. We thank J. J. Whitesell and J. C. Webb for technical assistance and Dr. J. E. Lloyd for helpful suggestions and for criticizing the manuscript. Supported by NSF grant GB 20749 and NIH grant NB 06459. Florida Agricultural Experiment Stations journal series No. 4356.

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