

Environmentally-induced Modification of the Chirp Length of Males of the True Katydid, *Pterophylla Camellifolia* (F.) (Orthoptera: Tettigoniidae)

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ABSTRACT

Small groups or colonies of males of the northern population of *Pterophylla camellifolia* (F.) can be characterized by the range and mode of the number of pulses in their chirps. During the first 1-2 wk after sexual maturity, many males produce chirps that are longer and more variable in length than chirps produced later in the season. Shortening of chirp lengths by katydids 1) isolated

from the sounds of conspecifics, and 2) forced to interact acoustically with a katydid producing shorter chirps, suggests that acoustical interaction among katydids effects change or stabilization of chirp length. A mechanism is proposed to explain short and long term changes in chirp length of *P. camellifolia* males.

The ability of insects to produce species-specific sounds appears to be genetically programmed and exposure to adult sounds is unnecessary (see reviews by Alexander 1960, 1968, Haskell 1961, Dumortier 1963, Marler 1963). Four types of evidence are available: 1) rearing male juveniles in isolation, 2) destroying auditory organs before they become functional, 3) comparing the sounds of offspring and parents of interspecific crosses, and 4) "natural experiments" resulting from maturation of insects that have not been exposed to sounds of adult conspecifics.

Males of some orthopterans modify their chirp rate (change in chirp length, intervals between chirps, or both) during acoustical interaction with 1 or more males. Changes in chirp rate are especially obvious for species in which males alternate or synchronize the production of chirps (Alexander 1960, Shaw 1968, Walker 1969). Therefore, for some Orthoptera, the definition of a species-specific sound includes predictable modifications in some sound parameters.

The nature of sound production of *P. camellifolia* males has been described (Fulton 1934, Alexander 1960, Shaw 1968) and analyzed in detail (Shaw 1968). Males produce 3 types of sounds: solo calling, alternating calling, and aggressive sounds (Fig. 1). Solo calling males are acoustically isolated from the sounds of other *P. camellifolia* males. In alternating calling, males, which are usually 7.5-15 m apart, alternate production of chirps.² Aggressive sounds consist of alternation of long chirps by katydids that are usually 60 cm or less from one another. For some males, chirps of alternating calling are 1 pulse longer than chirps of solo calling. Chirp lengths of aggressive sounds are usually 1-8 pulses longer than chirps of alternating calling.

The length of chirps (number of pulses, Fig. 1) of solo calling may vary within and among individuals of different colonies and populations. However, each individual, colony (first reported in this study), and population is characterized by a mode and range of

chirp pulse numbers (Alexander 1960, 1968, Shaw 1968, Shaw and Carlson 1969).

Insects that alternate or synchronize chirps may do so more or less continuously for at least several hours each evening. Long periods of acoustical interaction involving some modification in sound production seem to be likely situations for conditioning of acoustical response. Experiments by Pierce (1948) and Alexander (1960) emphasized the significance of the chirp lengths a katydid hears and responds to (i.e., alternates with) in determining a katydid's own chirp length. Both investigators, by repeated presentation of imitation chirps (Pierce: mouth imitations; Alexander: typewriter taps) were able to cause a 2-pulse katydid to produce 3-, 4-, and 5-pulse chirps in response to imitations of the same pulse number. This information plus knowledge of the nature of the variability of chirp length of *P. camellifolia* males during solo calling, alternating calling and aggressive sounds, led Alexander (1960) to speculate that the length (number of pulses) of a *P. camellifolia*'s chirp might be determined, at least in part, by the sounds the insect hears early in its adult life.

Objectives of this study were to investigate: 1) the nature of variation in chirp length of individuals and colonies in and around Ann Arbor, Mich., 2) whether range and mode of chirp lengths of individuals and colonies changed during the season, 3) the effect on a katydid's chirp length of isolation from the sounds of other katydids, and 4) the effect on a katydid's chirp length of acoustical interaction (i.e., alternation) with another katydid producing chirps of a different mode length.

METHODS AND RESULTS

Seasonal Changes in Chirp Length.—During the summer of 1960, field records of chirp lengths were kept for some *P. camellifolia* males located at different sites around Ann Arbor, Mich. Katydid's were identified by their calling sites (trees) and, when possible, by unique qualities of their calls. *P. camellifolia* males cannot fly, and most calling males seem to remain at approximately the same spot in a tree throughout their adult life.

Katydid trees were visited once or twice an evening at varying intervals which ranged from every evening

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² Chirps and pulses are illustrated in Fig. 1. A pulse is the sound produced by a single wingstroke; a chirp consists of 1 or more pulses. See Alexander (1967) for a consideration of definitions of these terms.

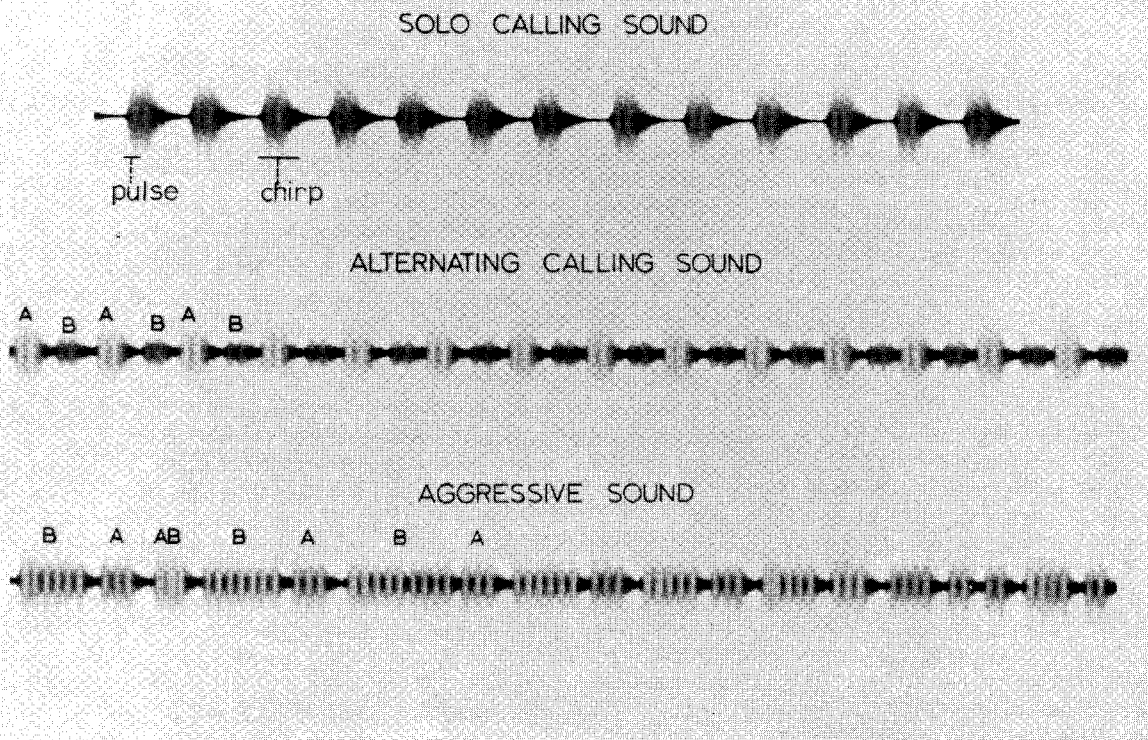


FIG. 1.—Oscillographs of calling and aggressive sounds of northern *P. camellifolia*. In alternating calling and aggressive sounds, chirps of the 2 different individuals are designated A and B. Adapted from Shaw (1968).

early in the season to once a week later in the season.³ At each visit, the lengths of successive katydid chirps were tabulated for 5 min.

The chirps of most katydids were longer and more variable in length during the first 2 wk of the season (Fig. 2). Alexander (1968) and I have found that *P. camellifolia* males initiate calling and increase chirp length more readily in response to human vocal imitations during the first few weeks of the adult katydid season. However, some katydids were never heard producing chirps longer than 2 pulses (e.g., L8, Fig. 2).

Most katydids began the season producing 2- to 7-pulse chirps, but were producing principally 2- and 3-pulse chirps in less than 2 wk (Fig. 2). After 2 wk, colonies or groups of katydids, which ranged from a few individuals to hundreds, could, on the basis of mode and range of chirp lengths of individuals making up each colony, be classified as follows: 1) 2-pulse colonies: mode chirp length of 2 pulses with range of 2-3 pulses; 2) 3-pulse colonies: mode chirp length of 3 pulses with range of 2-4 pulses; 3) 4-pulse colonies: mode chirp length of 4 pulses

with range of 3-5 pulses.⁴ Two-pulse colonies were the most common; 4-pulse colonies were encountered infrequently. Unfortunately, 4-pulse colonies were not encountered until after Aug. 14 and detailed singing records of individuals were not kept. However, records of Aug. 25 and Sept. 5 indicate that katydids in two 4-pulse colonies were still producing 3- to 5-pulse chirps.

The decrease in range and mode of katydid chirp lengths, and in katydids' capacities to respond to human vocal imitations, suggested a gradual increase in the threshold for increase in chirp length in response to acoustical stimuli (katydid or imitation chirps). The existence of some 4- and 5-pulse katydids and their restriction to colonies of individuals with similar chirp lengths suggested that the nature of acoustical interactions might be important in the establishment and maintenance of such a colony.

Effect of Acoustical Isolation on Chirp Length.—To test whether 3- and 4-pulse katydids could maintain their chirp length when not interacting acoustically with other katydids, 10 ♂, producing predominantly 3- or 4-pulse chirps, were collected and iso-

³ In Ann Arbor, Mich., *P. camellifolia* males call from the last wk of July or the 1st wk of August until the 1st or 2nd wk in October.

⁴ This classification of colonies of katydids appears to hold throughout the range of the northern populations of *P. camellifolia* (Alexander 1968, Shaw and Carlson 1969).

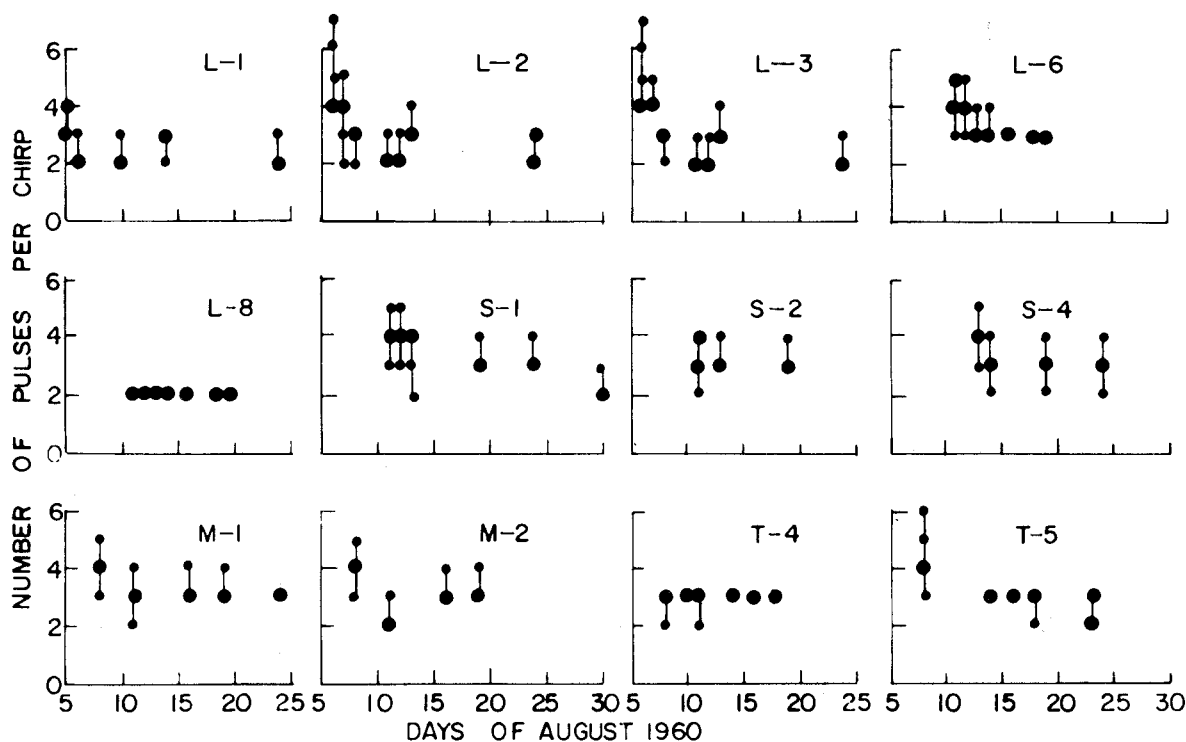


FIG. 2.—Field records of pulse numbers of chirps of selected males of northern *P. camellifolia*. All males were members of colonies and apparently within hearing distance of other katydids.

● — mode pulse number ○ — other pulse numbers

lated in different rooms. Katydid were visited at least once each evening to record their chirp lengths.

Of the 10 ♂, 5 chirped within 2-7 days after isolation. Trauma of capture and a strange environment may have been important factors in delaying chirping. However, lack of exposure to chirps of other katydids also could have been a factor.

After beginning to chirp, katydids N1, N2, and N3 produced only 2-pulse chirps. However, N7 and N8 produced 3-, 4-, and 5-pulse chirps for 2 evenings before converting to principally 2-pulse chirps. Katydid N7 and N8 were members of a 4-pulse colony, and exposure to long chirps of other katydids and/or producing and hearing their own long chirps may have facilitated their maintaining 3- to 5-pulse chirps for 2 evenings prior to production of only 2-pulse chirps.

In contrast, N2 and N3 were 3-pulse katydids from 3-pulse and 2-pulse colonies respectively. N1 was from a 4-pulse colony but variability in chirp length suggested that he had recently matured and, therefore, had experienced the chirps of other katydids for less than 2 wk. These factors, as well as not hearing himself or other katydids for 10 days prior to beginning to chirp in the laboratory, probably were responsible for his failure to produce chirps longer than 2 pulses after capture and acoustical isolation.

After converting to production of mostly 2-pulse chirps, all 5 katydids were exposed to electronically-

produced and human vocal imitations⁵ of katydid chirps varying in length from 1 to 6 pulses for 15-30 min each day for 1 wk. During this week, each katydid also was allowed to interact acoustically with another 2-pulse and a 4-pulse katydid. Each of the 5 katydids interacted at least twice with both 2-pulse and 4-pulse katydids for periods of 5-30 min. Each period of interaction was on different evenings. All katydids continued to produce principally 2-pulse chirps during and following exposure to acoustical stimuli.

These results suggest that katydids shorten their chirps when isolated from other katydid or imitation chirps. After shortening their chirps, they are refractory to lengthening chirps in response to katydid or imitation chirps.

It is possible that differences in chirp lengths among colonies reflect genetic or ontogenetic differences. However, except for N3's colony, katydids in colonies from which 3- and 4-pulse katydids were captured were still producing longer chirps after captured individuals had converted to 2-pulse chirps. Also, other 3- to 5-pulse katydids (e.g., N8, Table 2)

⁵ Vocal imitations of katydid chirps by the author were effective in stimulating increase in chirp length in some katydids encountered in the field or maintained in the laboratory throughout the katydid seasons during the summers of 1959 and 1960. Electronically-produced imitations were effective in stimulating increase in and maintenance of chirp lengths longer than 2 pulses of other katydids maintained in the laboratory before and after the time of conversion to 2-pulse chirps by katydids N1, N2, N3, N7, and N8.

Table 1.—Changes in mode pulse number of chirps during alternating calling.

Katydid	Exp. 1						
	August 1960						
	10	11	12	14	18	19	
N3p	(3)4(5) ^a	—	3(2)	2(3)	3(2)	2-3	—
N2	2	2	2	2	—	—	—
Katydid	Exp. 2						
	August 1960						
	25	26	27	28	29	30	31
N12	3(2)	3(2)	2(3)	2(3)	2(3)	2(3)	2(3)
N1	2	2	—	2	2	2	—

^a () — plus numbers other than mode.

captured at the same time or earlier, and used in studies of acoustic interaction, were still producing 3- to 5-pulse chirps at the time of conversion to 2-pulse chirps by the isolated katydid (Shaw 1968). This data plus the rapid shortening of chirps of all katydids when acoustically isolated in the laboratory suggests that acoustical interaction is responsible for maintenance of long chirps by katydids in the field.

Change in Chirp Length During Acoustic Interaction.—Observations in the field and in the laboratory suggested that a katydid also could modify his chirp length while acoustically interacting with another katydid. When 2 katydids, whose chirp lengths differ, are within alternating distance (7.5–15 m), the katydid with shorter chirps (the leader^b) often intermittently disrupts the pattern of alternation by temporarily chirping 2 or more times in succession (Fig. 3) (Shaw 1968). The katydid producing longer chirps (the follower) frequently shortens his chirp by 1 pulse. In contrast, alternating katydids with chirps of similar length (same pulse number) disrupt alternation and shorten chirp length much less frequently.

Acoustic interactions of katydids of different chirp lengths were evaluated in 2 field experiments. A caged 2-pulse katydid was placed 7.5 m from a 3-pulse katydid (Exp. 2), and a caged 2-pulse katydid was placed 7.5 m from a 4-pulse katydid (Exp. 1). The sites of caged katydids were visited twice each evening for 1 wk. Pulse numbers of caged and uncaged katydids were tabulated for 10 minutes at each visit. Two-pulse katydids did not alter the pulse number of their chirps. In contrast, the 3- and 4-pulse katydids shortened chirps frequently when chirping simultaneously with the 2-pulse katydid (Fig. 3). Within 3 days, the 3- and 4-pulse katydids were producing principally 2-pulse chirps (Table 1).

In the 2nd experiment, the 3-pulse katydid, N12,

was ca. 25 m from the nearest katydids of a 3-pulse colony. The 6 katydids in this colony continued to produce principally 3-pulse chirps for at least 1 wk following N12's conversion to principally 2-pulse chirps. In the 1st experiment, the 4-pulse katydid, N3p, was 1 of four 4-pulse katydids within 25 m of the introduced 2-pulser, N2. On the 3rd day (Aug. 12), N3p and P3, the closest katydid to N3p and N2 (ca. 9 m north of N3p and N2), were producing principally 3-pulse with some 2-pulse chirps. Katydids P2 (ca. 9 m north of N3p and 16 m north of N2) and P4 (ca. 16 m west of P3) were producing principally 4- and some 3-pulse chirps. By the 5th day (Aug. 14), N3p was producing principally 2-pulse chirps and P2, 3-pulse chirps. On Aug. 18 and 19, N3p increased the number of 3-pulse chirps, possibly as a result of N2 not chirping and the continual production of mostly 3-pulse chirps by P2. However, on both of these evenings, P3 was producing mostly 2-pulse chirps and P4 had reduced his mode pulse number to 3 pulses.

Although the tendency for katydids and colonies of katydids to reduce chirp length as the season progresses would suggest that katydids N12, N3p, P2, P3, P4, and P5 would reduced chirp length without the introduction of 2-pulsers N1 and N2, I contend that forcing these 3- and 4-pulse katydids to interact acoustically with a 2-pulse katydid facilitated shortening of chirp length. In the 1st experiment, the shortening of chirp length by N3p (and probably P3) because of acoustical interaction with the 2-pulser, N2, probably facilitated the eventual shortening of other katydids in the colony. The continual production of principally 3-pulse chirps by the colony near N12 and the existence elsewhere in Ames of two 4-pulse and five 3-pulse colonies at the time of shortening of chirp length by katydids N3p and N12 support this contention.

DISCUSSION

If isolation from the sounds of other conspecific males and possibly acoustical interaction with conspecifics of shorter chirp length results in more or less permanent shortening of chirp length of *P. camellifolia* males, what is the mechanism that brings this about? The results of an analysis of acoustical responses of *P. camellifolia* males to imitation and katydid chirps (Shaw 1968) suggests a mechanism that would explain short and long term changes in chirp length of this and possibly other species.

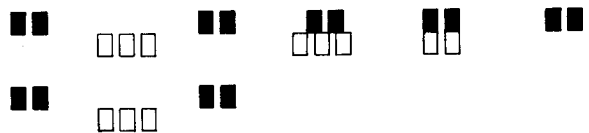


FIG. 3.—Diagrammatic illustration of an acoustical interaction between a 2-pulse male and a 3-pulse male of *P. camellifolia*. Second line is continuation of acoustical interaction of first line. ■■—2-pulse chirp of 2-pulse katydid. □□□ and □□—3- and 2-pulse chirps of 3-pulse katydid.

^b During alternation of chirps by pairs of katydid males, the "leader" intermittently chirps 2 or more times in succession; he also initiates chirping after both katydids have stopped chirping. In contrast, the "follower" only chirps following a leader's chirp (Baier 1930).

Table 2.—The effect of change in chirp pulse number during solo calling on chirp length and chirp interval.

Katydid	Temp (°C)	n	Chirps		Mean chirp interval	Difference in chirp	
			Pulse no.	Length in s		Length (s)	Interval (s)
N14	26.7	2	1p ^a	.10	.66	.13	.19
		26	2p	.23	.85		
N25	25.5	80	2p	.23	.62	.14	.13
		16	3p	.37	.75		
N1	28.3	6	1p	.10	.42	.12	.11
		49	2p	.22	.53		
N21	26.7	36	2p	.23	.53	.13	.07
		7	3p	.36	.60		
N8	26.7	60	4p	.48	.51	.12	-.02
		15	5p	.60	.49		

^a p = pulse.

Alternation of chirps by *P. camellifolia* males involves a slowing of chirp rate because 1 katydid is inhibited from chirping when another chirps. Inhibition or slowing of chirp rate also stimulates the production of longer chirps. This is expressed by the increased chirp length of the aggressive sound, and, for some katydids, the production of chirps that are 1-pulse longer during alternating calling than during solo calling. Acoustical isolation eliminates alternation and the inhibition necessary to stimulate the production of longer chirps. During acoustical interaction between katydids differing in mode chirp length, alternation is frequently disrupted by 2 katydids chirping simultaneously. Simultaneous chirping frequently is associated with shortening of chirp length by the katydid with the longer mode chirp length (Fig. 3). Successive simultaneous chirping during acoustical interaction of a 2-pulse and a 3- or 4-pulse katydid effectively eliminates inhibition or slowing of chirp rate and this is associated with relatively frequent shortening of chirp length by the 3- or 4-pulse katydid (Fig. 3).

The interval between 2 successive chirps of alternating katydids (response interval) is directly related to the katydid's chirp lengths and chirp intervals of solo calling. The longer the chirps of a katydid, the longer the chirp intervals of solo calling (Table 2), and the longer the response intervals of alternation (Shaw 1968). During alternation between 2 katydids differing in chirp lengths, the leader katydid, the one with shorter chirps, intermittently disrupts alternation by chirping before the other katydid terminates his chirp. When this occurs, a katydid that normally lengthens his chirp by 1 pulse during alternation is no longer delayed and his next chirp may be 1 pulse shorter (Fig. 3). Katydid responding to electronic imitations of chirps presented at varying chirp rates (Shaw 1968) shortened chirp lengths more frequently when the stimulus chirp overlapped the katydid's chirp than they did during soloing. In contrast to alternation in which an imitation or katydid chirp (stimulus chirp) inhibits a katydid from chirping and stimulates the production of longer chirps, a stimulus chirp that overlaps the chirp of another katydid appears to actively inhibit the production of longer chirps.

Thus, the mode chirp length of a katydid depends on the following: 1) a genetically determined threshold for increase in chirp length during acoustical interaction, and 2) the nature and effectiveness of acoustical interaction. When katydids first begin to call after maturation, they vary in their mode chirp length and in their response to imitation or katydid chirps. For example, L8 (Fig. 2) never was recorded producing chirps longer than 2 pulses and never increased his chirp length in response to mouth imitations of katydid chirps. Other katydids, for example, L2 (Fig. 2), produced up to 7-pulse chirps during calling and up to 12-pulse chirps in response to mouth imitations. If a katydid will respond to a stimulus chirp by producing chirps longer than 2 pulses, his ability to maintain a mode chirp length greater than 2 pulses will require an alternating partner that produces chirps longer than 2 pulses. Also, the katydids must be spaced so that the chirps of one will effectively inhibit the production of chirps of the other.

The most common cause, at least around Ann Arbor, Mich., for shortening of chirp length appears to be relatively large distances between katydids. Ann Arbor is near the northern limits of the range of *P. camellifolia* and the populations are relatively sparse. In addition, tree removal has disrupted the continuity of some colonies, and the disappearance of some individuals as the season progresses results in the loss of alternating partners.

P. camellifolia males that are disturbed jump to the ground and then walk until they encounter a vertical surface which they climb (Shaw 1968). Laboratory experiments have shown that following an aggressive encounter (production of aggressive sounds by 2 katydid males 60 cm or less from one another), 1 katydid moves silently away from the chirping "victor" (Shaw 1968). Thus, it is possible that a 2-pulse katydid possessing inherited or conditioned refractoriness to change in chirp length could move closer to a katydid producing longer chirps. Shortening of chirp length of one katydid of a colony because of acoustical interaction with a 2-pulse katydid could result in conversion to 2-pulse chirps of other members of the colony.

Results of experiments by Pierce (1948) and Alex-

ander (1960) suggest that shortening of mode chirp length may be reversible. Pierce (1948), after exposing a katydid to mouth imitations for several hours each day for 2 wk, and Alexander (1960), after exposing a katydid to imitations produced by tapping a typewriter for several hours each day for several consecutive days, reported that the katydids began to respond to 3-, 4-, and 5-pulse imitation chirps by producing 3-, 4-, and 5-pulse chirps respectively. These results apparently contradict my attempts to stimulate 2-pulse katydids to produce chirps longer than 2-pulses. The difference in results is related to the nature of stimulus (imitation chirp) presentation. In this investigation, electronically-produced and mouth imitation chirps were presented at variable rates. No attempt was made to maintain particular chirp lengths at rates with which the katydid could alternate efficiently for relatively long periods of time. The purpose of this experiment was not to attempt to reverse the direction of change in chirp length, but to indicate that these katydids had developed an increased refractoriness to increasing chirp length in response to imitation chirps of varying lengths.

In contrast, Alexander (1960) and presumably Pierce (1948) adjusted the rate of presentation of imitation chirps so that their 2-pulse katydids could alternate efficiently (i.e., be delayed by the total length of the long chirp). Both investigators stress the possible significance of producing chirps more or less in synchrony with the katydid chirps. However, I contend that it was the increased delay of the longer stimulus chirps which eventually resulted in production of longer chirps by the katydids. It is possible that simultaneous production of stimulus and katydid chirp immediately followed by katydid delay by a long stimulus chirp could be more effective than delay alone; but the results of my experiments (Shaw 1968) argue against synchronous production of katydid and stimulus chirp without successive delay being effective in bringing about lengthening of chirps by a katydid.

Pierce's (1948) and Alexander's (1960) results support my contention that under conditions of proper spacing, 3- and 4-pulse colonies could be maintained indefinitely. In other words, if a 2-pulse katydid that is refractory to increasing pulse length can, after some hours of efficient alternation with 3- or 4-pulse imitation chirps, be induced to maintain 3- or even 4-pulse chirps during alternating calling, couldn't field katydids under particular spacing conditions maintain 3- or 4-pulse chirps throughout the season as long as the number of individuals and spacing conditions were maintained?

Pierce's (1948) and Alexander's (1960) results also suggest that a 2-pulse katydid might be conditioned, by means of efficient alternation with 3- and 4-pulse stimulus chirps, to maintain 3- or 4-pulse chirps during solo calling for minutes, hours, or even days. In addition to planning such experiments, I predict their success.

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REFERENCES CITED

- Alexander, R. D.** 1960. Sound communication in Orthoptera and Cicadidae. Pages 38-92 in W. E. Lanyon and W. N. Tavolga, eds. Animal sounds and communication. Am. Inst. Biol. Sci., Washington, D. C.
1967. Acoustical communication in arthropods. *Annu. Rev. Entomol.* 12: 495-526.
1968. Arthropods. Pages 167-216 in T. A. Sebeok, ed. Animal communication. Indiana Univ. Press, Bloomington.
- Baier, L. J.** 1930. Contribution to the physiology of the stridulation and hearing of insects. *Zool. Jahrb.* 47: 151.
- Dumortier, B.** 1963. Ethological and physiological study of sound emissions in Arthropoda. Pages 583-654 in R. G. Busnel, ed. Acoustic behaviour of animals. Elsevier Publ. Co., New York.
- Fulton, B. B.** 1934. Rhythm, synchronism and alternation in the stridulation of Orthoptera. *J. Elisha Mitchell Sci. Soc.* 50: 263-7.
- Marler, P.** 1963. Inheritance and learning in the development of animal vocalizations. Pages 228-43 in R. G. Busnel, ed. Acoustic behaviour of animals. Elsevier Publ. Co., New York.
- Pierce, G. W.** 1948. The songs of insects. Harvard Univ. Press, Cambridge, Mass.
- Shaw, K. C.** 1968. An analysis of the phonoresponse of males of the True Katydid, *Pterophylla camellifolia* (Fabricius) (Orthoptera: Tettigoniidae). *Behaviour* 31: 203-60.
- Shaw, K. C., and O. V. Carlson.** 1969. The true katydid, *Pterophylla camellifolia* (Fabricius) (Orthoptera: Tettigoniidae) in Iowa: two populations which differ in behavior and morphology. *Iowa State J. Sci.* 44: 193-299.
- Walker, T. J.** 1969. Acoustic synchrony: two mechanisms in the snowy tree cricket. *Science* (Wash., D.C.) 166: 891-4.