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CALLING SONGS OF CRICKETS

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A knowledge of the intraspecific variation in cricket calling songs¹ and of the factors causing these variations is fundamental to the study of other aspects of the songs. For instance, work on the behavioral significance of the calling song must take into account the changes in calling song that occur with changes in certain environmental factors. Likewise, evaluation of interspecific differences and attempts to explain their origin are dependent upon a correct understanding of intraspecific differences. Finally, one working on the nervous control of singing must know what he has to explain before he can produce a thorough explanation.

The factors responsible for intraspecific variation in cricket calling songs can be classified conveniently under three headings: (1) current environment, i.e., the environment of the cricket at the time he is producing the song, (2) previous interactions with the environment, and (3) genetic factors.

Each of these will be discussed in turn, but first I will describe the mechanism of sound production in crickets and the physical characteristics of cricket calling songs.

MECHANICS OF SOUND PRODUCTION AND PHYSICAL CHARACTERISTICS OF THE CALLING SONG

Cricket calling songs are produced by rubbing together specialized tegmina. A small portion of the inner margin of the left tegmen is modified into a *scraper*, and

the right tegmen has a vein, called the *file*, which has a series of downward-projecting teeth. When the cricket stridulates the tegmina are elevated and alternately moved laterally and mesally, i.e., opened and closed. Sound is produced only during the closing stroke of the wing-motion cycle. Pierce (1948) first demonstrated this feature of sound production. He showed with motion pictures that a male *Gryllus* sp. moved its wings through three complete cycles (open-close, open-close, open-close) in producing a group of three pulses (a chirp). He observed that the wing-opening motions for a series of three pulses were not evenly spaced while the wing-closing motions were, there being a longer pause between the initial opening and closing than between the two subsequent ones. Since the three pulses of sound produced were evenly spaced, he concluded that they were the results of the wing-closing motions.

Using a stroboscope on two species of tree crickets (*Oecanthus quadripunctatus* and *O. argentinus*), I was able to demonstrate that when the wings were being moved 41 and 49 complete cycles per second, sound pulses were produced at the same rates (not double the rates as would be expected if both opening and closing were acoustically effective). The structure of the file gives indirect evidence that the closing rather than the opening stroke is the sound producing one. The lateral end of the file in tree crickets has a knob (fig. 1) which would act as a stop for the scraper moving along the file during the closing motion. Since the teeth project mesad in both *Oecanthus* and *Gryllus*, the scraper moves "against the grain" during wing closing. This may increase the amplitude of the vibration of the wings and cause the sound to be more intense.

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¹The calling song in crickets is made by the male when out of contact with other members of the same species. It serves to attract sexually responsive females, is produced for long periods, and is the type of cricket sound most commonly heard. For a general discussion of cricket sounds and their functions see the review by Alexander (1960).

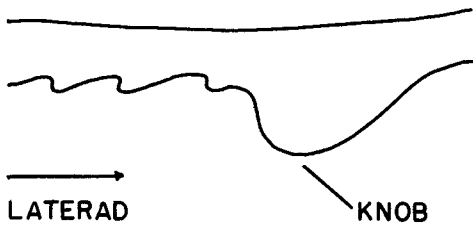


FIG. 1. Longitudinal section through the lateral end of the file of a tree cricket.

Since sound is produced during only a part of the wing-motion cycle, all cricket songs are constructed of sound *pulses*, which correspond to wing closures. If the cricket opens and closes its wings many times in succession, it produces a *trill* (fig. 2A). If it opens and shuts its wing a few times, pauses, and then does the same thing again, it produces a *chirp* (fig. 2B).

Pulse rate.—An important feature of cricket calling songs is that an individual

opening and closing its wings several or many times in succession usually does so at a uniform rate. When the song is analyzed, this characteristic wing-stroke rate is apparent from the *pulse rate* of the song. With a single exception, the calling song of each species with which I have worked has a single characteristic pulse rate (at a given body temperature). The exceptional species is *Nemobius carolinus*, in which the calling song usually contains two characteristic pulse rates. The usual song of *N. carolinus* is a continuous trill in which "smooth" (no audible periodic changes in intensity) portions alternate with "pulsating" (audible periodic changes in intensity occurring 7–13 times per second) portions. The pulse rate during the smooth portions is appreciably less than during the pulsating portions. For example, an individual at 19° C produced 57 p/s during the smooth portions of its song, and

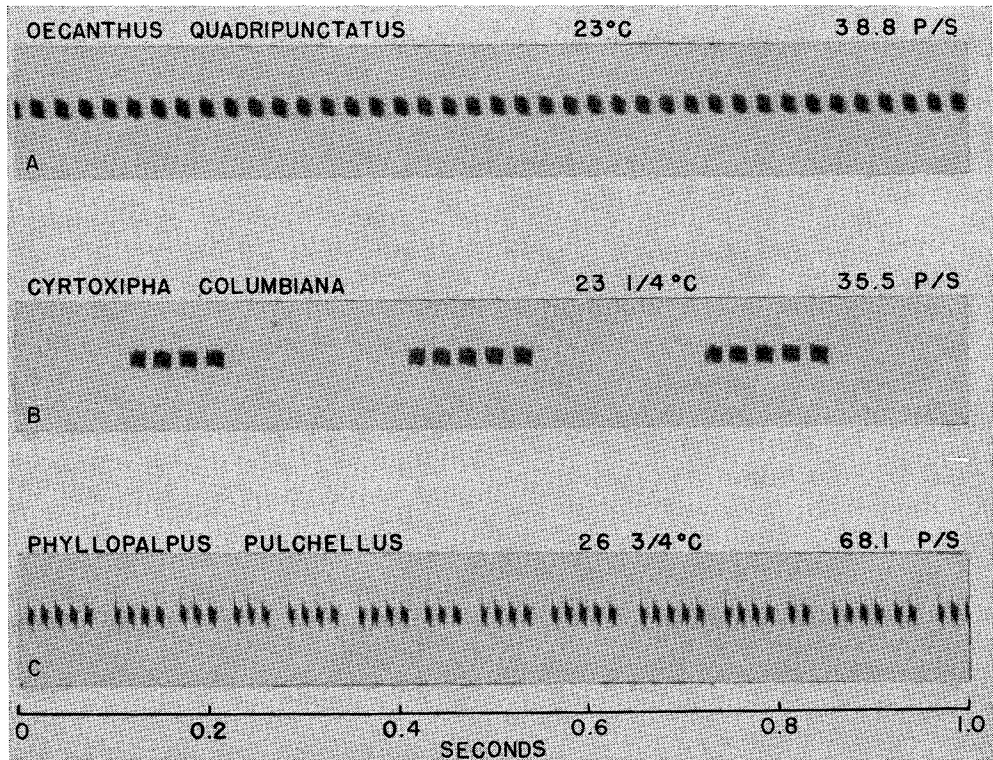


FIG. 2. Audiospectrograms of cricket calling songs. A. Portion of the trill of *Oecanthus quadripunctatus*. B. Three chirps of *Cyrtoxipha columbiana*. C. Portion of song of *Phyllopalpus pulchellus*.

70 p/s during the pulsating portions. (For audiospectrograms of smooth and pulsating trills in *carolinus*, see Alexander, 1957b.) The only other known case of a cricket alternating characteristic pulse rates is the Australian species, *Acheta commodus* (Alexander, 1962).

The calling songs of three other species with which I have worked have peculiarities associated with the pulse rate. *Phyllopalpus pulchellus* produces what sounds like an irregular and "ragged" trill. Analysis shows groups of pulses of highly variable length, with brief pauses between groups (fig. 2C). The rate at which the pulses are delivered during a pulse group is quite uniform, just as it is in typical chirping species in which pulse groups are more uniform in length and the pauses between groups are longer (e.g., *Cyrtoxipha columbiana*, fig. 2B).

Oecanthus fultoni and *O. rileyi* are exceptional in having pulse groups (chirps) composed of two or more lesser pulse groups. In *fultoni*, for example, the normal eight-pulse chirp consists of a group of two pulses closely followed by two groups of three pulses. (For a more extensive discussion of this phenomenon and an audiospectrogram illustrating it, see Walker 1962.) In spite of the complications introduced by the primary and secondary grouping of pulses, each of these two species still has a single characteristic pulse rate—the rate at which the pulses are delivered during the subgroups.

With the exception of *Nemobius carolinus*, then, we can talk about the pulse rate of a calling song.

Chirp rate.—In a few species of crickets, chirps are produced so regularly that measurements of chirp rate are reproducible. Chirp rate can be expressed as *chirps per minute*.

Frequency.—A final important physical characteristic of cricket calling songs is *frequency* (subjectively interpreted as *pitch*). The musical quality of cricket calling songs results from there being in any particular song a single strongly dom-

inant frequency of 2 to 10 kilocycles per second. The dominant frequency is evidently determined by the rate at which the scraper strikes the file teeth. If a cricket song has a dominant frequency of 4,000 cycles per second, the teeth are struck during wing closing at a rate of 4,000 per second. Since there are only about 20 to 200 teeth in the file, it is obvious that a single closing does not require much time. The dominant frequency normally decreases during each pulse, so the tooth-strike rate is evidently less toward the end of a wing closing. This results from the teeth being farther apart near the lateral end of the file, and also may indicate a slowing in the speed of wing movement.

The mechanism that allows tooth-strike rate to determine frequency is evidently this: the shock of each tooth strike causes a single vibration in the wing membrane, which in turn causes a single rarefaction and condensation in the air. The tegmina are highly damped, simple harmonic vibrators driven by the impacts of the scraper upon the teeth of the file. The action of the tegmina is similar to that of the sounding board of a piano. The tegmina and the sounding board vibrate at whatever frequency they are driven, and the result is a louder sound at the driving frequency.

An opposing theory of frequency determination was advanced by Pasquinelly and M.-C. Busnel (1954). They conclude that the stability and purity of pitch in the song of *Oecanthus pellucens* is best accounted for by considering the tegmina as resonators with well-defined constants. They propose that the two tegmina act as prongs of a tuning fork, and that when the tegmina move apart during a single vibration, the scraper is able to slip by one tooth of the file. The subsequent impact with the next tooth reinforces the next vibration of the wings. In their theory, then, the resonant frequency of the wing membranes determines the tooth-impact rate. This theory must be rejected for several reasons. First of all, experiments

in which the wing membrane was punctured (see below) did not result in a change in the dominant frequency of the song. The resonant frequency of the wing is certainly changed when the membrane is damaged, so no role of this frequency is indicated. Secondly, if the resonant frequency of the wings determines the frequency, changes in frequency with changes in pulse rate (see below) are difficult to account for. Nothing in the structure of the wings suggests the means of radical changes in resonant frequency. Finally, the wings are highly damped, that is, there is much resistance to their movement through the air. Any frequency other than the driving frequency would be expected to be of low intensity. For the resonant frequency to control the tooth-impact rate would require considerable action to be initiated by the resonating tegmina, and their highly damped state would make this unlikely.

Some experiments in which I mutilated the tegmina of specimens of *Oecanthus nigricornis* and *O. latipennis* give further support to tooth-impact rate being the normal determiner of frequency. Specimens which had produced normal songs were mutilated in the following ways: (1) hole cut in dorsal field of tegmen, (2) tip of dorsal field cut off, (3) lateral field of tegmen removed, and (4) functional file or functional scraper removed. In one group of each species the right tegmen was mutilated, and in another group of each species the left was mutilated. After a recording had been made of the song of an individual with one tegmen mutilated, the other tegmen was mutilated in the same manner as the first, and further recordings were made. Results of these experiments are described in detail in an unpublished thesis (Walker, 1957b), but may be summarized as follows: (1) In no case did an individual without a file or scraper produce a detectable song. (2) In no case in which a cricket sang with mutilated wings was there a deviation from the normal pulse rate of that species at that temperature. (3) In some cases individuals

singing with mutilated wings produced songs with broad frequency spectrums, there being no single strongly dominant frequency.

The first result confirms the importance of the file and scraper in sound production. The second shows the lack of influence of the resonance of the wings on the wing-stroke rate. The third requires closer scrutiny. A hole in the dorsal field usually had no effect on frequency; the tip of the tegmen being off usually had some effect; and the lack of a lateral field usually had a pronounced effect. These results are easily interpreted on the basis of the determination of frequency by tooth-impact rate, since the ability of a vibrator (the tegmen) to vibrate at a particular driven frequency (the tooth-impact rate) and none other varies with the rigidity of the vibrator. A rigid vibrator will vibrate at the driven frequency over its entire area, whereas a non-rigid vibrator will vibrate at different frequencies in different portions of its area. The mutilations rank in the same order in effect upon rigidity as in effect upon frequency. Puncturing the membrane had little effect upon the rigidity of the wing because only one of the supporting veins was cut. Cutting the tip from the wing disrupted the arched veins supporting the distal part of the dorsal field. The effect upon frequency was usually the introduction of additional frequencies with maintenance of the same dominant frequency as before—minor areas of the wing vibrated at other than the tooth-impact frequency. Cutting the lateral field from the wing reduced the rigidity drastically because much of the normal rigidity is a result of the lateral and dorsal fields lying in different planes. Removing the lateral field had a greater effect in *O. nigricornis* than in *latipennis*, probably because the dorsal field is narrower in the former and therefore more dependent upon the reinforcement of the outside edge. A final finding from the mutilation experiments was that at lower temperatures the effects of mutilations upon the song produced were less than at higher tempera-

tures. Since the tooth-impact rate is higher at higher temperatures, this finding may be explained by the decrease in ability of a damped vibrator (the tegmen) to vibrate at a driven frequency and none other as the frequency increases. The higher the driving frequency, the greater the stress upon the vibrator. The mutilated wings were weakened and often could not stand the stress of the higher frequencies at the higher temperatures; then instead of acting as simple harmonic vibrators, they vibrated in a complex fashion and produced a mixture of frequencies.

CURRENT ENVIRONMENT

Only three features of the current environment are known to influence the nature of the calling song. These are temperature, humidity, and sound. Only temperature has a pronounced and universal effect.

Temperature

The generalizations which will be made here as to the effects of temperature upon the nature of cricket calling songs are based principally upon studies of 20 species representing 5 subfamilies (references in parentheses give descriptions of the songs of the preceding species): OECANTHINAE—*Oecanthus niveus* (De Geer), *O. exclamationis* Davis, *O. fultoni* T. Walker, *O. rileyi* Baker, *O. latipennis* Riley (Walker, 1962); fast-trilling *O. nigricornis* F. Walker, slow-trilling *O. nigricornis*, *O. celerinictus* T. Walker, *O. argentinus* Saussure, *O. quadripunctatus* Beutenmuller, *O. pini* Beutenmuller (Walker, 1963); ENEOPTERINAE—*Orocharis saltator* Uhler (Alexander, 1960); GRYL-LINAE—*Gryllus rubens* Scudder (Alexander, 1957a); NEMOBIINAE—*Nemobius fasciatus* (De Geer) (Alexander and Thomas, 1959); *N. carolinus* Scudder (Alexander, 1957b); *N. ambiguus* Scudder (series of 10- to 20-pulse chirps with intervals between chirps usually lasting half as long to fully as long as a chirp); TRIGONIDIINAE—*Cyrtoxipha columbiana* Caudell, *Phyllopalpus pulchellus* Uhler (fig.

2); *Anaxipha pulicaria* (Burmeister) (trills of irregular duration, seldom longer than one second; intervals between trills very brief, usually less than 0.2 second); *A. imitator* (Saussure) (similar to *pulicaria* but trills more uniform in duration and intervals between trills longer, usually more than 0.2 second).

This is much too small a sample to inspire confidence that all the generalizations will hold for all crickets, but the generalizations work nicely for all the data presently available.

The data here presented are largely based on tape recordings made in controlled-temperature rooms. Most of the recordings of *Oecanthus* spp. were made with a Magnecord PT 63 (Midwestern Instruments, Tulsa 18, Oklahoma), and are in the Library of Animal Sounds, Ohio State University, Columbus. The remaining recordings were made with an Ampex 351 (Ampex Corporation, Redwood City, California), and are in the Tape Library of the Department of Entomology, University of Florida. All recordings were made with a D33 dynamic microphone (American Microphone Co., Pasadena, California) at a tape speed of 15 inches per second.

The test crickets were held individually in small cages. They were exposed to the test temperature at least one hour before their songs were recorded. Immediately after a song had been recorded, the temperature within the cage of that cricket was determined with an inserted thermocouple and a Leeds and Northrup potentiometer.

The frequency and pulse rate of the recorded songs were determined from audio-spectrograms made with a Vibralyzer or Sona-Graph (both manufactured by Kay Electric, Pine Brook, New Jersey). Chirp rate was determined with a stop watch.

Effect of temperature on pulse rate.—Warm crickets sing at a higher pulse rate than cool crickets. Changes in pulse rate with temperature seem to follow a uniform

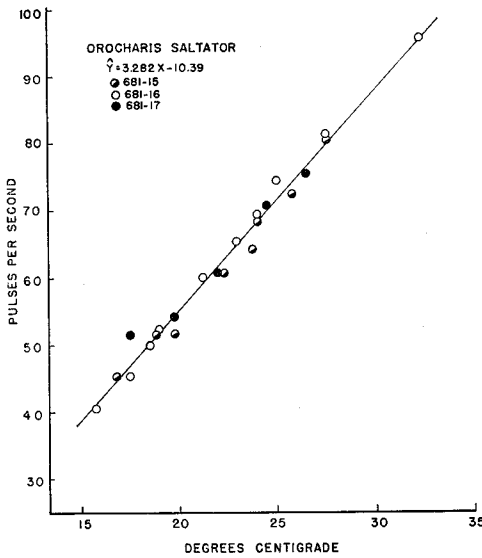


FIG. 3. Effect of temperature on pulse rate in *Orocharis saltator*. Three individuals (681-15, 16, 17) from Alachua County, Florida, April-May 1961.

pattern which can be described by three generalizations.

First, for any species of cricket the rate of change in pulse rate with temperature is constant—i.e., a graph with pulse rate plotted against temperature forms a straight line. Table 1 summarizes the relationships between pulse rate and temperature for the 19 species of crickets for which sufficient data are available. The detailed data for nine of these species are shown in figs. 3-8. The remaining data are in other papers (Walker, 1962 and 1963).

Although straight lines adequately describe the effect of temperature on pulse rate in all data I have seen from crickets, Frings and Frings (1957) give data showing a logarithmic relationship in a tettigoniid, *Neoconocephalus ensiger*. On the basis of the cricket data now available, it seems likely that if a deviation from a linear relationship is found, it will be at the extremes of temperature and will probably consist of slightly higher than expected pulse rates at extremely low temperatures,

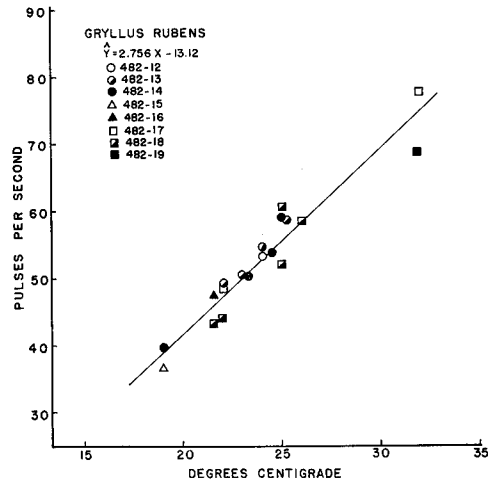


FIG. 4. Effect of temperature on pulse rate in *Gryllus rubens*. Eight individuals from Alachua County, Florida, May-June 1961.

or lower than expected pulse rates at extremely high temperatures.

The second generalization is that the higher the pulse rate at a given temperature, the greater the rate of change—i.e.,

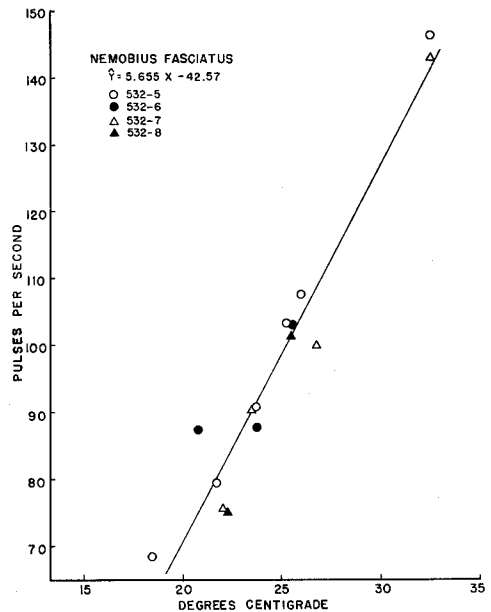


FIG. 5. Effect of temperature on pulse rate in *Nemobius fasciatus*. Four individuals from Alachua County, Florida, June 1961.

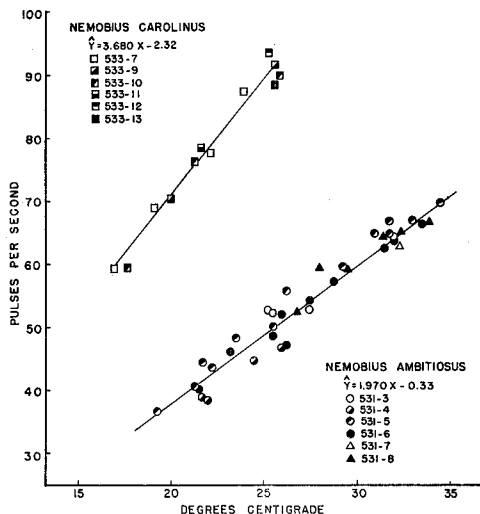


FIG. 6. Effect of temperature on pulse rate in *Nemobius carolinus* and *N. ambitiosus*. Six individuals of each from Alachua County, Florida, May-June 1961.

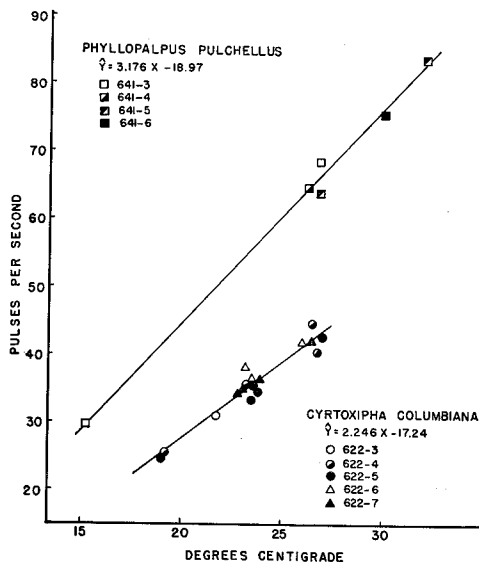


FIG. 7. Effect of temperature on pulse rate in *Phyllopalpus pulchellus* and *Cyrtoxipha columbiana*. Specimens from Gainesville, Florida, July 1961.

the steeper the regression line on a graph with pulse rate plotted against temperature. Fig. 9 shows the regression lines for the 19 species. In general, the steeper lines lie above the more gently sloping ones.

The third generalization describes a tendency suggested in fig. 9: If one extrapolates the regression lines downward, they tend to converge at 4° C and 0 p/s (pulses per second). While it is quite apparent that the regression lines do not come to a point, they cluster most closely at about 0 p/s, and they reach this pulse rate at temperatures close to 4° C. The last column in table 1 shows that the calculated temperatures at which the expected pulse rate is 0 range from 0.6 to 7.7° C. The mean is 4.1, with a standard deviation of 1.8. It is likely that the more extreme deviations from the mean are at least in part a result of inadequate data. The species which deviate widely from the mean are mostly those in which pulse rate is more difficult to determine accurately (the chirpers) and those in which the data available are scanty. I do not mean to say that the lines would converge on a single point if experimental error were eliminated—I only

wish to suggest that the tendency to converge might be more pronounced with more accurate or more extensive data.

If one concedes that there is a tendency for the extrapolated pulse rate in cricket

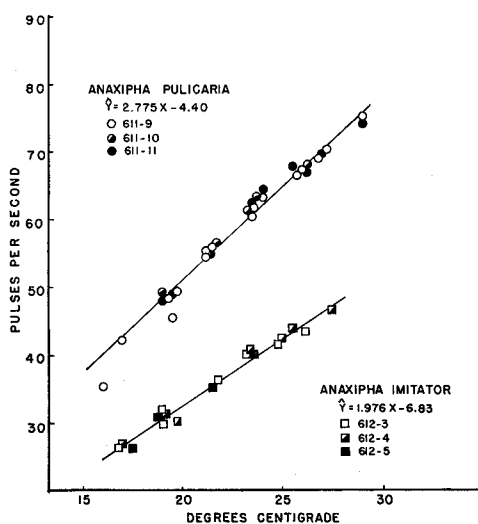


FIG. 8. Effect of temperature on pulse rate in *Anaxipha pulicaria* and *A. imitator*. Specimens from Gainesville, Florida, May 1961.

TABLE 1. Relation of temperature and pulse rate in the calling songs of 19 species of crickets

Species	Detailed data	Regression line ¹		X when $\hat{Y} = 0$ (° C)
		a	b	
OECANTHINAE				
<i>O. niveus</i>	Walker, 1962	-13.52	3.400	4.0
<i>O. exclamationis</i>	Walker, 1962	-10.48	3.654	2.9
<i>O. fultoni</i>	Walker, 1962	- 4.16	2.237	1.9
<i>O. latipennis</i>	Walker, 1962	- 8.94	2.515	3.6
fast <i>O. nigricornis</i>	Walker, 1963	-17.74	3.415	5.2
slow <i>O. nigricornis</i>	Walker, 1963	-13.12	2.659	4.9
<i>O. celerimictus</i>	Walker, 1963	-19.00	3.348	5.7
<i>O. argentinus</i>	Walker, 1963	-12.42	2.556	4.9
<i>O. quadripunctatus</i>	Walker, 1963	- 8.21	1.969	4.2
<i>O. pini</i>	Walker, 1963	- 7.56	2.088	3.6
ENEOPTERINAE				
<i>O. saltator</i>	Fig. 3	-10.39	3.282	3.2
GRYLLINAE				
<i>G. rubens</i>	Fig. 4	-13.12	2.756	4.8
NEMOBIINAE				
<i>N. fasciatus</i>	Fig. 5	-42.57	5.655	7.5
<i>N. carolinus</i> ²	Fig. 6	- 2.32	3.680	0.6
<i>N. ambitiosus</i>	Fig. 6	- 6.97	2.232	3.1
TRIGONIDIINAE				
<i>C. columbiana</i>	Fig. 7	-17.24	2.246	7.7
<i>P. pulchellus</i>	Fig. 7	-18.97	3.176	6.0
<i>A. pulicaria</i>	Fig. 8	- 4.40	2.775	1.6
<i>A. imitator</i>	Fig. 8	- 6.83	1.976	3.5

¹ $\hat{Y} = a + bX$ where \hat{Y} is expected pulses per second and X is degrees Centigrade.

² The regression line given is for the fast pulse rate.

calling songs to reach 0 at 4° C, several useful implications are evident. One such implication is that if the pulse rate of a calling song is known for any one temperature, the pulse rate at any other temperature can be predicted with reasonable accuracy. All that must be done is to assume that the regression line would pass through 4° C at 0 p/s. A second implication is that the ratio between pulse rates of any two species should remain constant regardless of temperature. Thus if species *A* sings twice as fast as species *B* at 15° C, it should sing twice as fast at 20° C, 25° C, or 30° C. A third and similar implication is that wing-stroke rate will always double between 15 and 26° C or between 20 and 36° C, etc.

Effect of temperature on chirp rate.—Only two of the species studied have chirp rates regular enough to justify detailed consideration of the effect of temperature. These are *Oecanthus fultoni*, the snowy

tree cricket, and *Oecanthus rileyi*, a western species closely related to *fultoni*.

In a recent paper (Walker, 1962) I discuss the chirp rates of these two species and give detailed data showing the relation of chirp rate and temperature in laboratory recordings of Ohio *fultoni*. Fulton (1925) gives detailed data (31 field observations, 14 indoor observations) on the chirp rate in Oregon *rileyi*.

The three generalizations made about pulse rate and temperature seem to apply equally well to the chirp rate in *fultoni* and *rileyi*. The relationship between temperature and chirp rate is definitely a linear one. The regression line for Ohio *fultoni* is $\hat{Y} = -38.61 + 8.208X$ (\hat{Y} = expected chirps per minute; X = degrees Centigrade), and the formula of the line drawn by eye to fit Fulton's data for Oregon *rileyi* is $Y = -15.99 + 5.099X$. The faster chirper (*fultoni*) has the steeper line (a slope of 8.2 as compared with one of 5.1

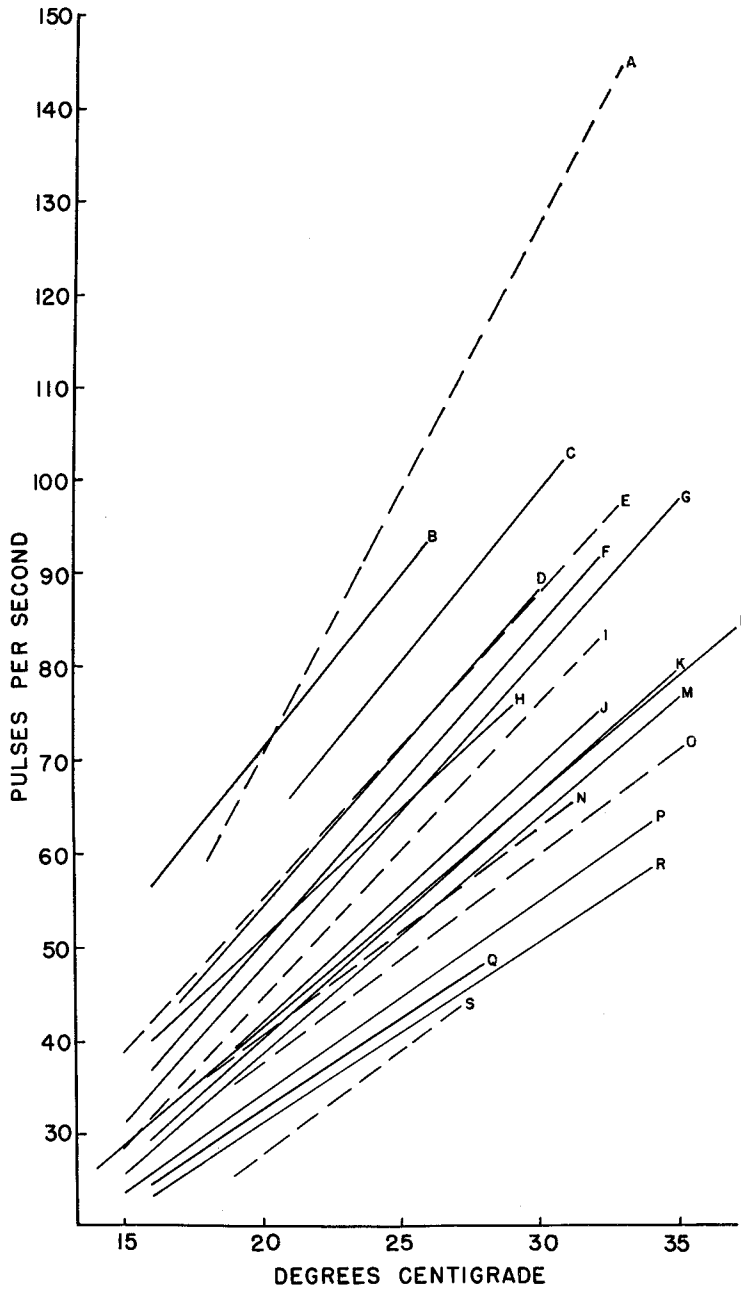


FIG. 9. Regression lines summarizing the effect of temperature on pulse rate for 19 species: A. *Nemobius fasciatus*, B. *N. carolinus*, C. *Oecanthus exclamationis*, D. *O. niveus*, E. *Orocharis saltator*, F. fast-trilling *Oecanthus nigricornis*, G. *O. celerinictus*, H. *Anaxipha pulicaria*, I. *Phyllopalpus pulchellus*, J. *Gryllus rubens*, K. slow-trilling *O. nigricornis*, L. *O. latipennis*, M. *O. argentinus*, N. *O. fultoni*, O. *N. ambitiosus*, P. *O. pini*, Q. *A. imitator*, R. *O. quadripunctatus*, S. *Cyrtixipha columbiana*. Dashed lines represent species in which the pulses are produced in short sequences.

in *rileyi*). Furthermore, extrapolation reveals *fultoni* reaching 0 chirps/minute at 4.7° C and *rileyi* reaching 0 ch/m at 3.2° C. The mean is 4.0° C!

Since the chirps of these species are made up of fairly uniform numbers of pulses, one might think that generalizations valid for pulse rate would automatically be valid for chirp rate. This is not so, however, because the intervals between chirps would not *a priori* follow the same relations with temperature as the duration of the chirps (which would be determined by pulse rate and number). An analogous situation is the relation of pulse duration and pulse interval, which will be discussed below.

Effect of temperature on frequency.—Frequency varies with temperature, but not in the regular way that pulse rate and chirp rate do. Two generalizations can be made.

First, frequency increases with increases in temperature, at least at low and moderate temperatures (10 to 25° C). The exact relationship varies from species to species, and in some cases the rate of increase of frequency with temperature decreases or becomes zero.

To illustrate the *types* of relationships which may exist between temperature and frequency I will give detailed data for five species. Fig. 10 shows two species, *Nemobius ambitiosus* and *Gryllus rubens*, in which the relation between temperature and frequency is approximately linear throughout the range of temperatures in which singing normally occurs. This graph and the others in this series have pulse rate rather than temperature on the abscissa. Since pulse rate and temperature have been shown to be linearly related, one scale is easily converted to the other. Pulse rate is used because it makes possible the use of some recordings for which accurate temperature data are unavailable. The frequency in *ambitiosus* rises quite steeply with temperature (or pulse rate), while in *rubens* the rate of change is very low. Only by following the data for individuals of

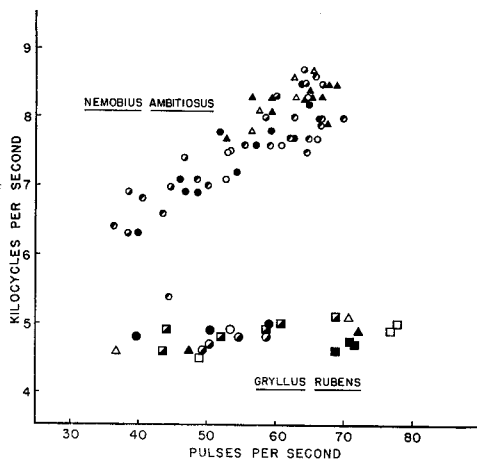


FIG. 10. Relationship between pulse rate and frequency in *Nemobius ambitiosus* and *Gryllus rubens*. Symbols refer to individuals and are keyed the same as in figs. 4 and 6.

rubens can one be certain that a rise in frequency with temperature is demonstrated in fig. 10. The data for *Oecanthus argentinus* (fig. 11) shows, at higher temperatures, a gradual decrease in the rate of increase of frequency with temperature. Of the 19 species in which frequency was studied, 14 show either no decline or a slight decline in rate of increase at the higher temperatures—i.e., the relationships are similar to those illustrated in figs. 10 and 11.

The remaining species show much more pronounced reductions in the rate of increase in frequency at higher temperatures. In *Oecanthus pini* (fig. 12) the rate falls rapidly above 28° C (= 50 p/s), and in *Orocharis saltator* (fig. 13) there seems to be no further increase in frequency above 27° C (= 78 p/s).

Fig. 14 shows the approximate relation of frequency and pulse rate in nine species of crickets. Elsewhere (Walker, 1962, 1963) I give lines for ten species of *Oecanthus* and some additional detailed data. As yet I have found no way to predict the shape of the frequency curve, even if all other relationships are known.

The other generalization which can be made as to the effect of temperature upon

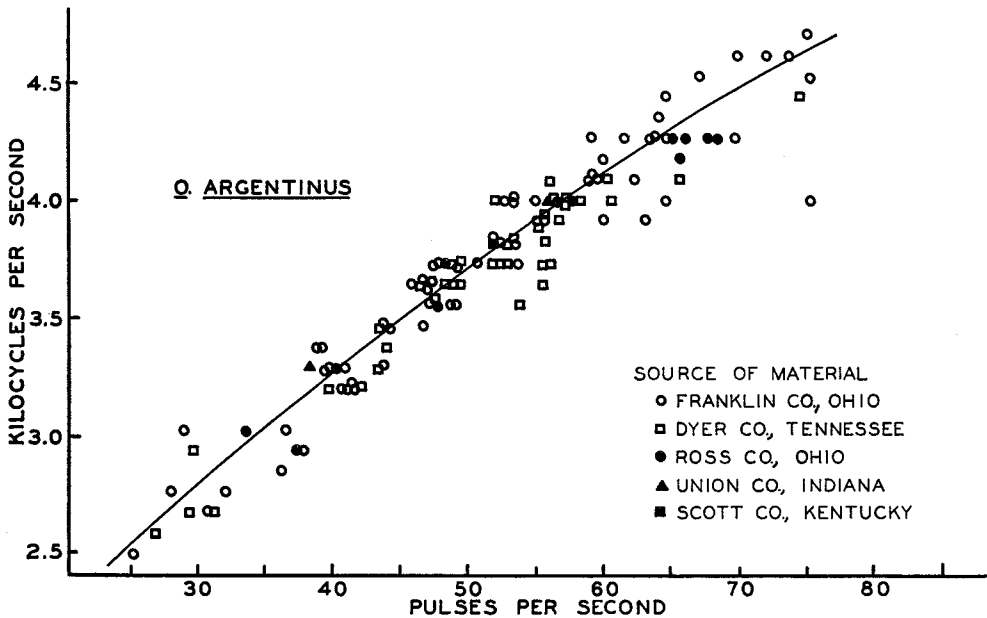


FIG. 11. Relationship between pulse rate and frequency in *Oecanthus argentinus*. Curve fitted by eye.

frequency is that with changes in temperature, the per cent change in frequency is always less than the per cent change in pulse rate. If the pulse rate doubles (i.e., increases by 100%) with a given rise in temperature, the frequency increases no more than 57% and usually considerably less (e.g., approximately 7% in *Gryllus rubens*).

Discussion of temperature effects.—Since the tooth-strike rate (frequency) does not increase as rapidly as wing-stroke rate (pulse rate), increases in pulse rate with increases of temperature must be a complicated phenomenon. It is obvious that doubling the pulse rate involves something other than merely doubling all speeds in the wing-stroke cycle. I will refer to two mechanisms which could account for the failure of frequency to double when pulse rate doubles. First, at higher temperatures the time spent in wing closing (i.e., striking teeth) may become a larger proportion of the total time involved in a wing-stroke cycle. In terms of speed of wing movement rather than time, this mechanism means

that as pulse rate increases, the speed during wing opening may increase more rapidly than does the speed during wing closing. The number of teeth struck would not have to change.

The second mechanism is that at higher pulse rates the wings may move a shorter distance (i.e., fewer teeth may be struck). If the wings move a shorter distance, they can make more round trips per unit time without a proportional increase in speed. Neither the proportion of time spent in the closing or opening part of the wing-stroke cycle nor the speed of wing movement would have to change. Additional mechanisms can be postulated, but they introduce complications not required by the evidence presently available.

I have developed no completely satisfactory technique for determining duration or speed of wing opening or wing closing or for determining number of teeth struck. However, by slowing down the tape recordings (usually to 1½ ips) and changing the settings on the Sona-Graph (or Vibralyzer), audiospectrograms with greatly

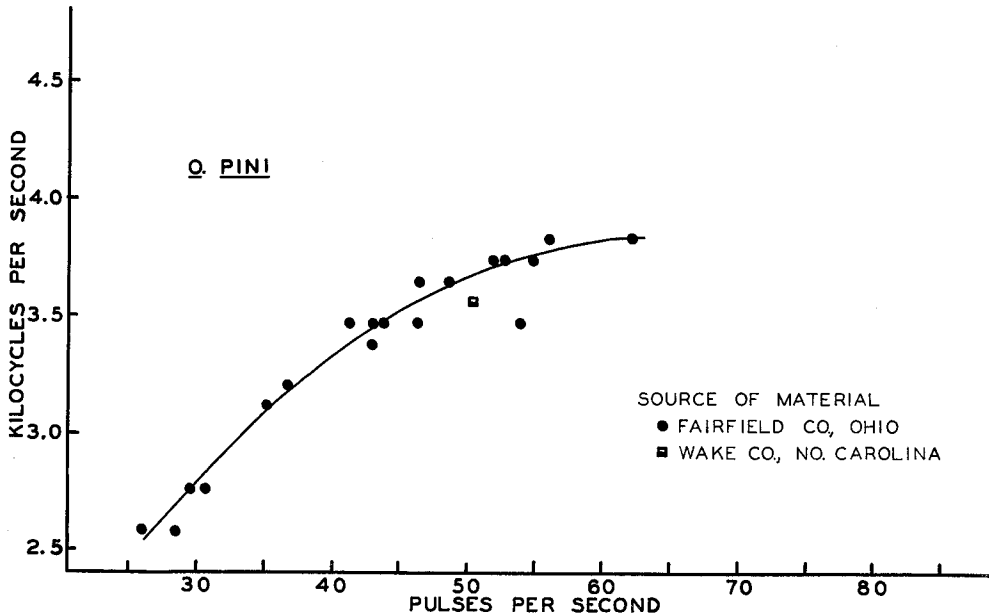


FIG. 12. Relationship between pulse rate and frequency in *Oecanthus pini*. Curve fitted by eye.

expanded time scales can be produced. The duration of pulse and pulse interval can then be measured. The difficulty with this method is that the pulse duration indicated on the audiospectrogram depends in part on where the marking intensity of the Sona-Graph is set. Furthermore, the transition from sound to silence (pulse to pulse interval) is seldom sharp, perhaps because of reverberations or background noise at the time of recording. If the time scale of the audiospectrogram is expanded even further, paired marks become evident which correspond to the fundamental waves of the original signal—and therefore to tooth strikes. The number of paired marks in a pulse should be equivalent to the number of tooth strikes. However, it is usually difficult to make a reliable count because the marks may gradually diminish toward the end of the pulse, and where the count is terminated becomes a matter of subjective interpretation.

In spite of difficulties in interpreting some audiospectrograms with expanded time scales, I have been able to reach some tentative conclusions as to the me-

chanics of increase in pulse rate without corresponding increase in tooth-strike rate.

In some species the first suggested mechanism (change in relative speed or duration of wing closing and wing opening) seems to act alone in producing the effect—at least throughout the range of temperatures investigated. For instance in *Oecanthus argentinus* the proportion of time spent in wing closing becomes progressively greater as temperature increases (fig. 15). At $17\frac{1}{2}$, $23\frac{1}{4}$, and 31° C, approximately 53, 65, and 76% of the total time of the wing-stroke cycle is spent during wing closing. The number of tooth-strikes involved in each pulse was calculated from the pulse duration and the frequency. At $17\frac{1}{2}$, $23\frac{1}{4}$, and 31° C, the pulses involved approximately 46, 51, and 50 tooth-strikes. No reduction in number of tooth-strikes per pulse at higher temperatures is indicated.

Analyses of songs of *Oecanthus niveus* revealed a situation like that in *argentinus*. The number of tooth-strikes per pulse was approximately the same at $23\frac{1}{2}$, $26\frac{1}{2}$, and 31° C, and wing closing occupied a greater

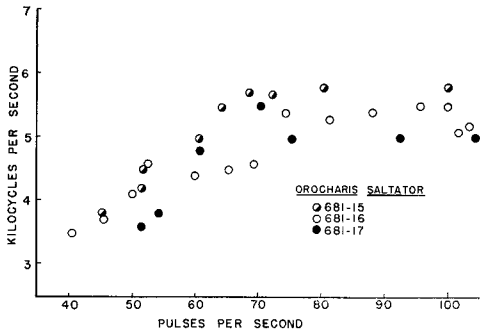


FIG. 13. Relationship between pulse rate and frequency in *Orocharis saltator*.

were approximately 55 tooth-strikes per pulse. At the same two temperatures wing closing occupied 66% and 81% of the total wing-stroke cycle. It was calculated that the speed during wing closing increased only by 6.5%, whereas the speed during wing opening increased by 129%.

It also was calculated that if only the first mechanism had been involved (as is apparently the case in *O. argentinus* and *O. niveus*), the speed of the opening wing stroke would have had to increase by 1,219%! This illustrates an important consideration—if only change in relative speed of wing opening and wing closing is involved in explaining frequency and pulse rate relationships, in some species the speed of the wings during opening would have to become exceedingly high at the higher pulse rates. In *rubens*, for instance, the speed

proportion of the wing-stroke cycle at the higher temperatures.

Both suggested mechanisms were found to be in operation in *Gryllus rubens*. At 21½° C approximately 65 tooth-strikes per pulse were counted, while at 31¼° C there

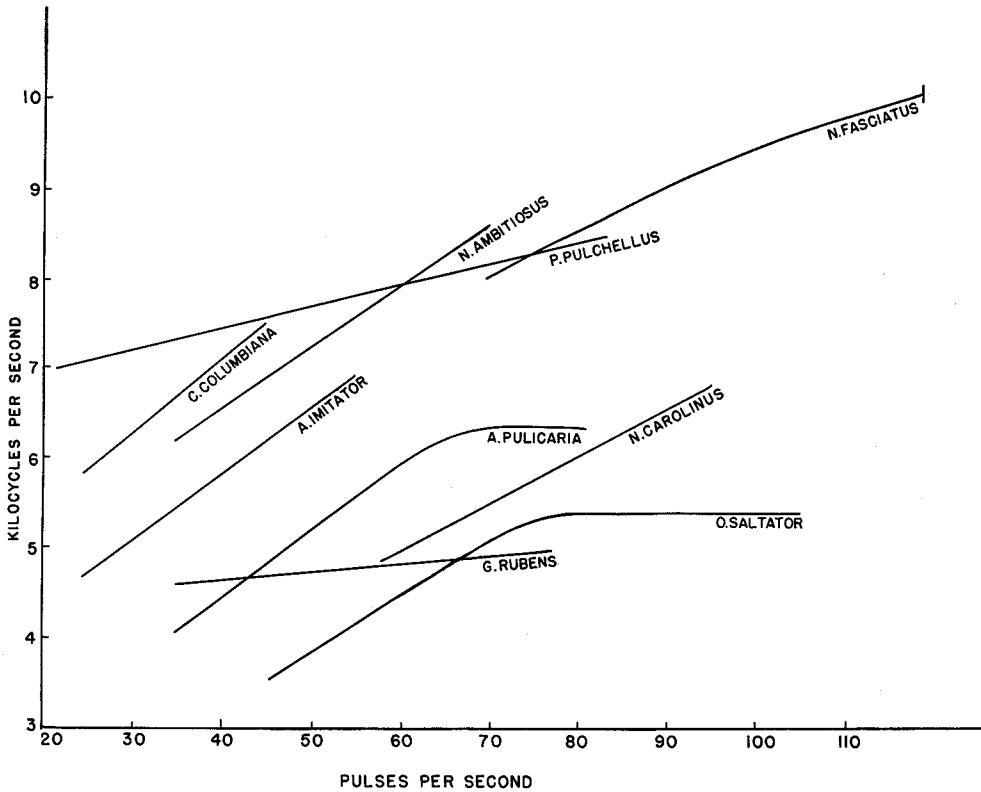


FIG. 14. Summary of relationships between pulse rate and frequency for nine species. All lines were fitted by eye.

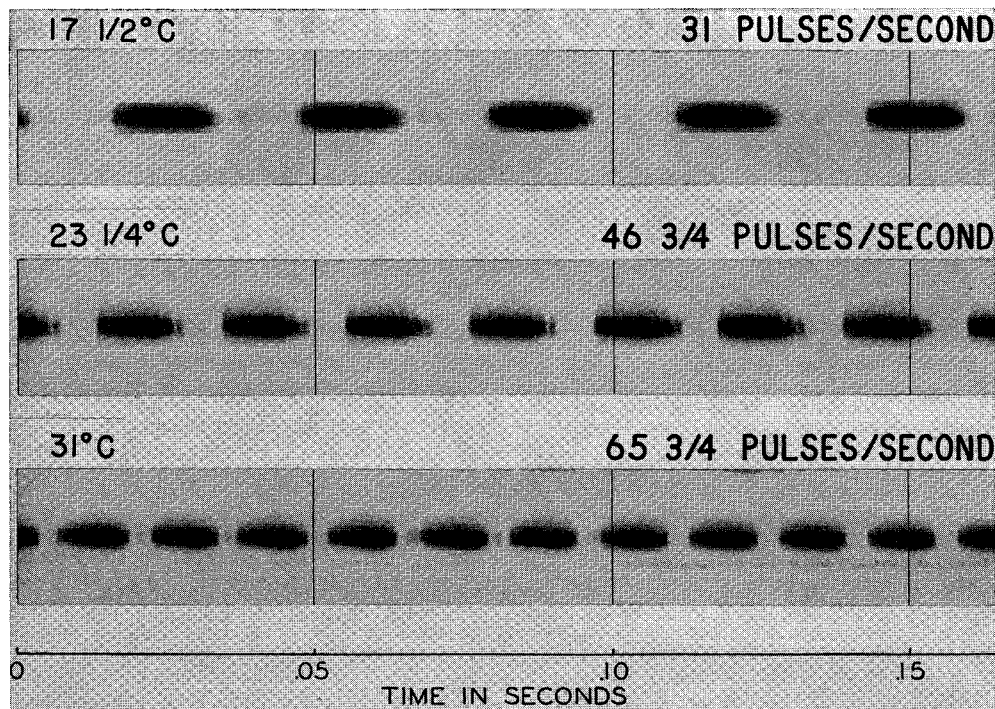


FIG. 15. Audiospectrograms showing changing relationship between pulse and pulse interval with changing temperature and pulse rate in *Oecanthus argentinus*.

would approach infinity at about 80 p/s (33°C).

Both mechanisms were found to be involved in *Orocharis saltator*. Other analyses were made, but the results were not clear-cut. In no case, however, was there evidence of the operation of the second mechanism without the first being involved also. Analyses of both fast and slow portions of the song of *Nemobius carolinus* showed that at least the first mechanism is involved in the lagging increase of frequency with increase of pulse rate (both slow and fast) at higher temperatures. However, the switch from slow to fast pulse rates at the same temperature is of interest because the switch occurs with no apparent change in tooth-strike rate and only the second mechanism (fewer teeth struck) appears to be involved.

In summary, I think it likely that the speed of wing opening always increases more rapidly than the speed of wing closing

with increases in temperature. In some species fewer teeth are struck per pulse at the higher temperatures. In other species there is evidently no such reduction.

Factors involved in the evolution of temperature effects.—The lack of understanding of the physiological (including neurological) events responsible for the wing movements of stridulating crickets complicates speculations as to the evolution of the temperature effects discussed above. Studies of wing-stroke rates in flying insects, however, suggest that the effects found in crickets are not the only ones which could occur from a physiological standpoint (Chadwick, 1953).

The linear relationship between pulse rate and temperature may be wholly or partly attributable to the female. Pulse rate is frequently the feature that causes the female to go to the song of her own species instead of another. It has been demonstrated that the particular pulse rate

to which a female cricket is most likely to respond varies with temperature in the same manner as does the pulse rate produced by the male (Walker, 1957a). In other words, the mechanism which determines response in the female and the mechanism which determines wing-stroke rate in the male show similar responses to temperature. It is possible that the similarity is a result of the same physiological process timing both mechanisms. It seems more likely, however, that one or both mechanisms have changed from the original state in response to the selective pressure caused by the other.

The relationships between chirp rate and temperature in *Oecanthus fultoni* and *O. rileyi* are probably a consequence of the prior evolution of the pulse rate relationships which they resemble (see Alexander, 1962, for evidence that trill production probably preceded the production of regular chirps). In *fultoni* and *rileyi* the chirp has evidently come to have the same behavioral impact on the female that the pulse has in other species (Walker, 1957a). Thus the response mechanism in the female may be the same as in other species. If so, it would result in the selection of males which chirp by the rules that apply to pulse production in other species.

The question of why frequency changes relatively little (as compared to pulse rate and chirp rate) with changes in temperature may be answered in two ways. First of all, the relationships between frequency and temperature may simply be by-products of other forces—for instance, the evolution of the pulse rate relationships and the physiological and mechanical interactions of stridulation. A second explanation is that the frequencies most easily heard have exerted selective pressure on the frequencies produced. The only experimental work on cricket auditory thresholds I know of is that by Wever and Vernon (1959). Using *Gryllus* sp. (probably *pennsylvanicus*; sex not stated), they found that the sensitivity of the tibial tympani of the forelegs was greatest at about 5,000

cps (cycles per second). The sensitivity was substantially less at 4,000 and 7,000 cps and at all other frequencies tested. It is not surprising that *Gryllus* spp. produce songs of about 5,000 cps. There has been no work done as to how the auditory sensitivity of crickets varies with temperature. If it varies slightly or not at all, the relatively slight changes in frequency with temperature and the decline in the rate of increase at higher temperatures in some species may be a result of selection against crickets which produce frequencies outside the range of frequencies most easily heard by other individuals of the species.

Humidity

Several authors have suggested that humidity may have some influence on the nature of cricket calling songs, but I know of no published reports of carefully controlled experiments designed to test the effects of humidity.

I have done two series of such experiments. The first was in 1956, using four species of *Oecanthus*. Individuals of *O. rileyi*, fast-trilling *O. nigricornis*, *O. celerinictus*, and *O. quadripunctatus* were confined in small chambers through which dried or humidified air could be passed. With the dried air, the relative humidity in the chamber was maintained at less than 13%; with the humidified air, the relative humidity was greater than 93%. Humidity was determined with an electric hygrometer. Each day the songs were recorded and the chamber humidities alternated. Immediately after each recording the temperature and humidity within the chamber were determined. At temperatures near 24° C, eight individuals (all four species represented) sang two or more times under both high and low humidities. No consistent differences were found in frequency, pulse rate, or chirp rate in songs produced at the contrasting humidities.

The second series of experiments was done in 1961 in a controlled-temperature, controlled-humidity room (Parce Bioclimatic Chamber, Parce Engineering Co.,

TABLE 2. *Effect of humidity upon pulse rate*

Species and individual	Relative humidity	Approx. temp. ¹ ° C	Actual p/s minus expected p/s ²		Equivalent temperature change (° C) ³
			Differences	Av.	
<i>N. ambitiosus</i>					
531-5	60 ± 5	27° C	2.3, 2.5, 2.0	2.6	-0.4
	25 ± 5		2.2, 1.2	1.7	
531-5	95 ± 5	31° C	-0.2, -0.7, -0.5	-0.5	-0.2
	20 ± 5		-1.1, -1.1, -0.4	-0.9	
531-8	60 ± 5	27° C	0.6, 0.9, 1.1, 0.9, 1.7	1.0	-0.1
	25 ± 5		0.6, 1.0, 1.4, 0.4	0.8	
531-11	95 ± 5	31° C	-5.1, -5.3	-5.2	-0.3
	20 ± 5		-6.9, 4.8	-5.8	
<i>A. pulicaria</i>					
611-12	95 ± 5	27° C	3.7, 3.4, 3.6, 4.8	3.9	-0.7
	60 ± 5		1.2, 2.0, 2.4	1.9	
	25 ± 5		1.4, 1.9, 1.9, 3.3, 1.7	2.0	
<i>O. quadripunctatus</i>					
582-44	60 ± 5	27° C	2.2, 3.6, 5.0, 5.3	4.0	-0.2
	25 ± 5		3.2, 4.9, 1.2, 5.0	3.6	
582-45	95 ± 5	27° C	3.8, 3.2, 3.9, 3.4	3.6	-0.6
	60 ± 5		1.9, 1.9, 2.9, 2.3, 2.8	2.4	
582-53	95 ± 5	31° C	5.6, 4.6	5.1	0.0
	20 ± 5		4.4, 4.4, 6.1	5.0	
582-56	95 ± 5	31° C	3.5, 5.0	4.2	+0.2
	20 ± 5		3.9, 5.3	4.6	

¹ The exact temperature varied slightly depending on the position of the cage and the phase of the temperature control cycle. The temperature used in calculating expected pulse rate was that taken in the cricket's cage immediately after its song was recorded. Temperature within any particular cage varied no more than $\pm 0.3^\circ$ C during the temperature control cycle.

² Expected pulse rates were calculated from the formulae given in table 1.

³ The equivalent temperature change indicates the temperature change which would be expected to have the same effect on pulse rate as the humidity change being tested.

Harlingen, Texas). The test crickets were held in individual screen-covered cages. The water vials were removed (except at 95% R.H.), and humidity and temperature were held at the desired level at least an hour before songs were recorded. Immediately after a song was recorded the temperature in the singer's cage was determined with a thermocouple. Both the tape recorder (Ampex 351) and the potentiometer were kept outside the test room, so their performance could not be influenced by the conditions in the test room. Test crickets were exposed to high (95 ± 5), medium (60 ± 5), and low (25 ± 5) relative humidities at 27° C, and high (95 ± 5) and low (20 ± 5) humidities at 31° C.

Table 2 shows the results of this second series of tests. All individuals are listed that were recorded at least twice under two or more humidities at a single temperature. In *Nemobius ambitiosus* there is a slight reduction in pulse rate at the lower humidities. The degree of reduction is variable, and there is always some overlap between the pulse rates produced at the two humidities. The average effect of lowered humidity, however, is a reduction in pulse rate equivalent to that produced by a decrease in temperature of 0.25° C. A somewhat similar effect is seen in *Anaxipha pulicaria*, although here pulse rate appears to be no lower at 25% R.H. than at 60% R.H. The pulse rate at both of these humidities, however, is

substantially lower than at 95% R.H. A temperature drop of about 0.7° C would be required to match the effect. In *Oecanthus quadripunctatus*, no effect is demonstrated in three of the individuals; however, individual 582-45 at 27° C shows a consistently lower pulse rate at 60% R.H. than at 95% R.H.

These experiments make it clear that crickets sometimes sing at slightly reduced pulse rates at low humidities. However, the reduction is so slight as to be easily obscured by individual variation (see below) and by minor variations in temperature. Apparently the amount of reduction is highly variable (from slight to none), sometimes even in the same individual under the same external conditions.

The most logical explanation of these results is that the effects of humidity are a result of reduced body temperature caused by increased evaporation. The amount of water lost per unit time (and hence the reduction in body temperature) is variable even under uniform external conditions because of changes in the cricket and its water balance. The degree of body temperature depression postulated on the basis of pulse rate determinations is compatible with the depressions measured directly in insects by various workers (see Edney, 1957, pp. 73-77).

The effects of humidity revealed in these experiments are too small to be of any significance under field conditions. Microclimatic variations in temperature would have much greater effects than the most extreme variations in humidity. Furthermore, most crickets sing only under humid circumstances—at night and/or in humid microhabitats.

Sound

Natural sounds have no influence on the nature of most calling songs; except that in several species that chirp rhythmically, neighboring males synchronize their chirping. In these species, then, the *phase* of chirping is affected by the sounds of neighboring males. Species that sometimes syn-

chronize include *Oecanthus fultoni*, *O. rileyi*, and *Cyrtoxipha columbiana*.

The chirp rate is also influenced by sound in these species. Two males may sing at slightly different rates alone, but of course sing at the same rate when they synchronize. In experiments on the mechanism of synchronization, I played recorded songs to *O. fultoni* and discovered that individuals could increase their chirp rate by as much as 50 chirps per minute or decrease it by as much as 35 chirps per minute in synchronizing with the recordings. Synchronization resulted from changes in the chirp interval and in the number of pulses per chirp. Pulse rate was unchanged.

Other Factors

No other features of the current environment are known to affect the nature of the calling song. Many features, however, are important in determining whether the calling song is produced. Examples are light intensity, wind, rain, and mechanical disturbance.

Although these are not agents contributing to intraspecific variation in calling songs, two of these—light and wind—will be discussed.

Light.—While many crickets seldom sing except in the dark or at very low light intensities (e.g., *Oecanthus niveus*, *Orocharis saltator*), some sing regularly both day and night (e.g., *Oecanthus quadripunctatus*, *Nemobius ambitiosus*), and others seldom sing except during the day (e.g., *Phyllopalpus pulchellus*). I have tape recordings of calling songs made in the light and in the dark under controlled conditions for individuals of six species—*Gryllus rubens*, *Oecanthus quadripunctatus*, *Phyllopalpus pulchellus*, *Nemobius ambitiosus*, *N. carolinus*, and *N. fasciatus*. "Dark" recordings were made with a small, shielded, red light (less than 1 foot candle incident light at the cages—no reading on a General Electric Model 8DW40Y16 light meter). "Light" recordings were made with the room lights on (at least 8 foot

candles incident light at the cages). Analyses of the recordings revealed no differences in the calling songs produced under these two light intensities.

Analyses of field recordings (made with a Magnemite 610E) of *Oecanthus quadripunctatus*, *O. argentinus*, *O. nigricornis*, and *O. celerimictus* made in sunlight and at night revealed no differences in calling song which were not attributable to temperature differences. A final evidence that light does not alter the calling song is that the songs of *O. argentinus* and *O. quadripunctatus* did not change when the singing crickets were viewed with a stroboscope.

Air currents.—Allard (1930a) suggested that wind might affect the chirp rate of *Oecanthus fultoni* by increasing evaporation from the cricket, thereby cooling it and lowering the chirp rate. In a later article Allard (1930b) reported he had directed a small electric fan toward a caged individual of *fultoni* singing in his bedroom. In seven trials, when the fan was turned on the chirp rate consistently increased from about 172 to about 185 ch/m. When he directed the fan toward a cricket singing outdoors, there was no change in chirp rate.

I was unable to show any effect of wind in controlled experiments with *O. nigricornis*, *O. latipennis*, and *O. fultoni*. The crickets were placed in a cylindrical wire cage (14-mesh screening) in a controlled-temperature room. When a cricket began to sing, a recording was made; then a small electric fan was directed toward the singer, and another recording was made. The temperature within the cage was measured with a thermocouple before and after the fan was turned on. Air velocity was determined with a Hastings Air-Meter (Hastings Instrument Co., Inc., Hampton, Virginia) by inserting the probe through a hole in the top of the cage after the recording with the fan turned on had been made. Air velocity was measured at the place in the cage where the cricket had been singing. When the fan was off, the room's temperature control apparatus caused an

TABLE 3. *Effect of air currents upon the calling songs of three tree crickets. Relative humidity approximately 60%*

Species	° F	Air speed ft/min	p/s	cps	ch/m
<i>O. nigricornis</i>	77	15	67¼	3,800	—
	77	300	67½	3,800	—
<i>O. latipennis</i>	72	15	46¼	2,800	—
	72	350	47	2,800	—
<i>O. fultoni</i>	76	15	50½	2,700	166
	77	200	51½	2,700	169

air velocity of about 15 feet/minute in the cage.

Table 3 shows the data for the three individuals which continued to sing after the fan was turned on. In no case was the song with the fan turned on significantly different from the song with the fan off. Allard's (1930b) results with *O. fultoni* may perhaps be explained on the basis that the air the fan circulated was slightly warmer than the air about the cricket with the fan off. On the other hand, perhaps the cricket was synchronizing with some rhythmic sound produced by the fan (see above).

PREVIOUS INTERACTIONS WITH THE ENVIRONMENT

There has been almost no experimental work on the possible influence of "previous environment" upon the nature of the calling song. I am of the opinion that under natural conditions previous interactions with the environment contribute very little to intraspecific variation in cricket calling songs.

Perhaps the most impressive evidence which bears on this matter is that of species with more than one generation per year. In these species, successive generations often develop and mature under quite different environmental circumstances. Nevertheless, the calling songs of successive generations are indistinguishable. For example, in central Ohio, *Oecanthus argentinus* overwinters in the egg stage, hatches about June 1, matures about July 1, and sings until the middle of August. A second

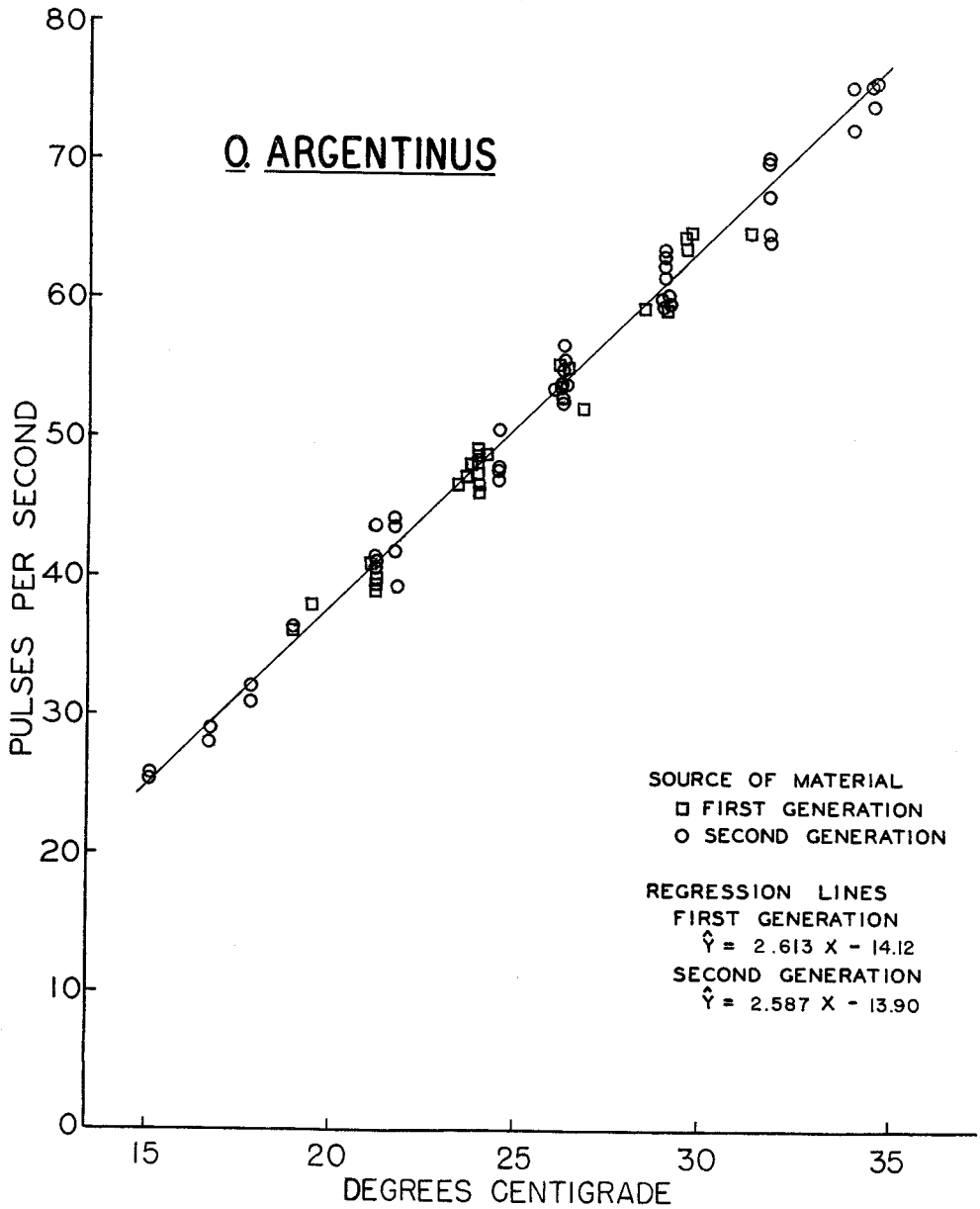


FIG. 16. Effect of temperature on pulse rate in the first and second generations of *Oecanthus argentinus*, Franklin County, Ohio, 1956.

generation starts as eggs in July and August, matures about the middle of September and sings until frost. Fig. 16 shows that the relation between temperature and pulse rate is apparently the same in the two generations.

In *Drosophila*, Chadwick (1953, p. 592) found that the wing-beat frequency during flight changed with age. This suggests there might be some effect of age on a cricket's wing-stroke rate during stridulation; however, comparisons of wing-stroke

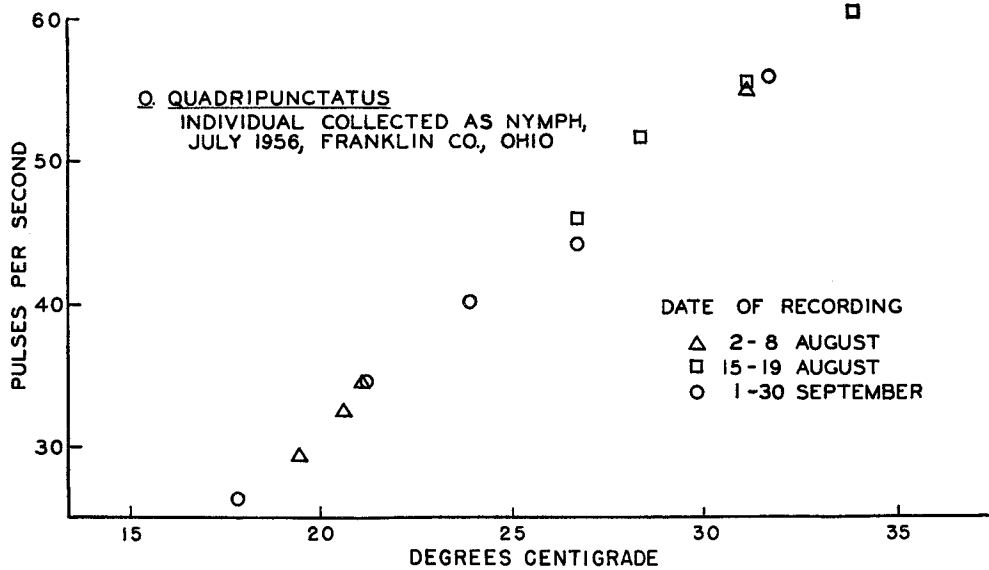


FIG. 17. Lack of change with age in relationship between temperature and pulse rate, as shown by laboratory recordings of an individual of *Oecanthus quadripunctatus*.

rates of the same cricket at various ages show no effect of age on wing-stroke rate. Fig. 17 shows the pulse rates produced by an individual of *Oecanthus quadripunctatus* during two months of singing, a period probably longer than the stridulating life of the average cricket.

One type of event related to aging does have some influence upon the nature of the calling song. Damage to the tegmina may result in a less intense sound and/or a sound with a broader frequency spectrum. The effect of natural damage ("normal wear and tear") to the tegmina is of the same type as described above in the discussion of mutilation experiments.

Crickets often sing for several hours with only brief pauses. At 50 pulses per second, the wings move back and forth 180,000 times per hour. It would seem that fatigue might develop and cause the cricket to move its wings more slowly, but there is no evidence of such an effect. In the only specific attempt I have made to check the effect of fatigue, a tree cricket (*Oecanthus argentinus*) was recorded while it sang con-

tinuously for 30 minutes. During this recording the pulse rate did not change.

A final question concerning the effects of previous environment is the possibility that conditioning may influence the nature of a cricket's calling song. Typical calling songs are produced by crickets which have never heard another individual of the species sing. This is demonstrated each year in every species which overwinters only in the egg stage. That the typical song can be produced without conditioning is of course no proof that conditioning cannot influence the nature of the song.

GENETIC FACTORS

Whenever the songs of individuals from a local species population are recorded under identical conditions, consistent differences between the songs can be found. Furthermore, consistent differences can sometimes be found in the songs produced by geographically separated populations of a single species. If my contention is valid that previous environment normally has little influence on the nature of the call-

ing song, these differences are principally genetically determined.

Examples of individual variation in calling songs may be found in the figures used to illustrate the first part of this paper. In fig. 13, individual 681-15 of *Orocharis saltator* produced frequencies consistently higher than those of 681-17. Other examples are in fig. 10 (*Gryllus rubens*, 482-13, low; 482-14, high), fig. 5 (*Nemobius ambitiosus*, 532-5, fast; 532-7, slow), and fig. 6 (*N. fasciatus*, 531-4, slow; 531-5, fast). Two extreme examples among tree crickets are illustrated elsewhere (Walker, 1962, fig. 2).

Geographic variation in the song is usually slight. In studies of the songs of tree crickets from all over the United States (Walker, 1962, 1963), I found easily detected geographical variation in the song of only one species, *Oecanthus fultoni*. This species chirps at an appreciably higher rate on the West Coast than in the East. It seems likely that the occurrence of a slow-chirping sibling species (*O. rileyi*) on the West Coast is responsible for the evolution of a faster chirp rate in the western populations of *O. fultoni*.

ACKNOWLEDGMENTS

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SUMMARY

The basic units of structure of cricket calling songs are pulses of rather pure frequency produced by closures of the elevated tegmina with scraper and file engaged. The dominant frequency of the pulse is determined by the tooth-strike rate. Pulses may be produced in long sequences (*trills*) or in shorter sequences (*chirps*). Within a trill or chirp the pulses are usually produced at a uniform pulse rate, and in some cases chirps are produced at a uni-

form chirp rate. The pulse rate is the wing-closing rate, and the chirp rate is the rate at which groups of wing closures occur. Factors causing intraspecific variation in the characteristics of the calling song are considered under three headings: (1) current environment, (2) previous interactions with the environment, and (3) genetic factors.

Most contemporaneous environmental factors which affect the cricket (e.g., rain, wind, light) are important only as to whether or not the cricket produces the calling song, and do not affect the nature of the calling song. Temperature has a pronounced effect. The following generalizations concerning changes in cricket calling songs with the changes in temperature are based on studies of 20 species representing 7 genera and 5 subfamilies: (1) Pulse rate changes with temperature at a constant rate. (2) The higher the pulse rate at a given temperature, the greater the rate of change in pulse rate with changes in temperature. (3) If the pulse rate produced at any one temperature is known, the approximate rate of change can be predicted by assuming that the pulse rate would be 0 at 4° C. (4) In species which produce uniform chirps separated by uniform intervals, the above three generalizations apply to chirp rate as well as pulse rate. (5) Frequency may change with temperature (and pulse rate) at a constant rate, or at higher temperatures the rate of increase may decline so that there is little or no further increase in frequency. (6) The per cent change in frequency is always less than the per cent change in pulse rate with a given change in temperature. Low humidity may reduce the pulse rate slightly, probably as a result of increased cooling by evaporation. In crickets that chirp at a uniform rate, sound may influence the chirp phase, as shown by synchronization of neighboring individuals, and chirp rate, as shown by exposing chirping individuals to recordings of songs at higher or lower chirp rates.

Previous interactions with the environment are apparently seldom involved in

intraspecific variation in calling song. Succeeding generations, which develop under different environmental conditions, produce identical calling songs. Neither fatigue nor age appears to affect the nature of the calling song. Damage to the stridulatory apparatus may result in a less intense song and in a greater range of frequencies, but does not ordinarily affect pulse rate or chirp rate.

Genetic differences probably account for most cases of individual variation and geographical variation in calling song. Such variations are usually minor.

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