

Effects of Temperature, Humidity, and Age on Stridulatory Rates in *Atlanticus* spp. (Orthoptera: Tettigoniidae: Decticinae)¹

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ABSTRACT

In *Atlanticus gibbosus* Scudder the wing-cycle rate during stridulation is a linear function of temperature: $\dot{y} = 1.35 T - 9.56$ ($T = ^\circ\text{C}$; $r^2 = .99$). In *A. dorsalis* (Burmeister) the tooth-strike rate during stridulation can be described approximately as either a linear or an exponential function of temperature: $\dot{y} = 33.55 T - 268.32$ ($r^2 = .96$) or $\text{Ln } \dot{y} = .065 T + 4.523$ ($r^2 = .96$). Humidity

and aging had statistically significant but ecologically unimportant effects on stridulatory rates. In *A. gibbosus* the wing-cycle rate at low humidities ($25 \pm 5\%$ RH) was reduced to the extent expected from 0.7°C evaporative cooling. In *A. dorsalis* aging beyond ecological life expectancy caused an increase in tooth-strike rate and the occurrence of gaps in the tooth-strike sequence.

The calling songs of male crickets and katydids (Gryllidae and Tettigoniidae) function in sexual pair formation, and different species singing together have different songs. At least in temperate latitudes, the singers of one generation generally must produce their songs without having had the opportunity to hear the songs of the previous generation. It is therefore not surprising that individuals are able to produce the song that is characteristic of their own species even if they have heard only the songs of other species. Indeed, the calling songs of crickets and katydids are apparently as directly related to genotype as is genital structure except that ambient temperature causes large change in the speed, though not the pattern, of stridulatory movements. I recently (Walker 1975) summarized the effects of temperature on stridulatory wing-cycle rates in crickets and katydids and previously (Walker 1962) reported on the effects of humidity and age on calling songs of crickets. This paper considers for the first time the effects of these latter 2 factors on tettigoniid calling songs and presents the first data for temperature effects on tettigoniid tooth-strike rate—i.e., the rate of movement during the acoustically effective portion of the tegminal movement cycle.

METHODS

Males of *Atlanticus gibbosus* Scudder and *A. dorsalis* (Burmeister) were collected in Alachua County, Fla., held individually in small cages, and tape recorded in a bioclimatic chamber. During all tests temperatures were within 0.5°C of the set point of the thermostat. During tests of the effects of temperature, the set point was changed daily with the direction of change reversed every 1–4 days. Except for 2 individuals of *A. dorsalis*, the extremes included temperatures above and below the range in which singing occurred. In temperature tests, humidity was monitored but not controlled. It varied between 55 and 85% RH and between 3 and 27 millibars saturation deficit.

The humidity tests involved only *A. gibbosus* and were done at the same time as previously reported tests with crickets (Walker 1962). Humidity was

controlled $\pm 5\%$ RH of the set point of the hygrostat. On 3 successive days the chamber was set at 27°C and 60, 25, and 95% RH. Twenty-four days later, on 2 successive days, it was set at 31°C and 95 and 25% RH. Each individual was tape recorded 2–5 times each day.

The tape recordings used to assay the effects of age were those made during studies of the effects of temperature and humidity.

Prior to tape recording sessions, the katydids had at least one hour to adjust to chamber conditions. A remote-controlled Ampex® 351 tape recorder, outside the chamber, was used to record the calling songs. Immediately after a song was taped, the temperature within the cage was measured with a thermocouple. The tape recorded songs were analyzed with a Kay Sona-Graph® audiospectrograph.

For each species the stridulatory rate selected for detailed analysis was the one showing least variability within and among individuals under the same environmental circumstances. The calling songs of all katydids consist of repeated acoustical units, called *phonatomes*, that correspond to wing-movement cycles (Walker and Dew 1972). In *A. gibbosus* 8 to 12 phonatomes are produced in quick succession to form a *phrase* (Fig. 1A), and the phonatome rate within a phrase is nearly constant for any given set of environmental conditions. For example, measurements of such rates in different phrases in the same tape recording had a coefficient of variation of 0.7% (based on analyses of two phrases in each of 20 recordings). Tooth-strikes could not be discriminated in audiospectrograms of songs of *A. gibbosus*. In *A. dorsalis* (Fig. 1B) phonatomes are produced at irregular intervals, but the average tooth-strike rate within the prolonged portion of the phonatome has low variability. The coefficient of variation for measurements of average tooth-strike rates in the prolonged portions of different phonatomes in the same tape recording was 3.5% (based on analyses of 2 phonatomes in each of 20 tape recordings). Tooth-strike rate changes during the prolonged portion of each phonatome and the changes are most rapid at either end; however, calculating the tooth-strike rate using only tooth-strikes No. 11–20 did not decrease the variance in the values obtained for single tape recordings.

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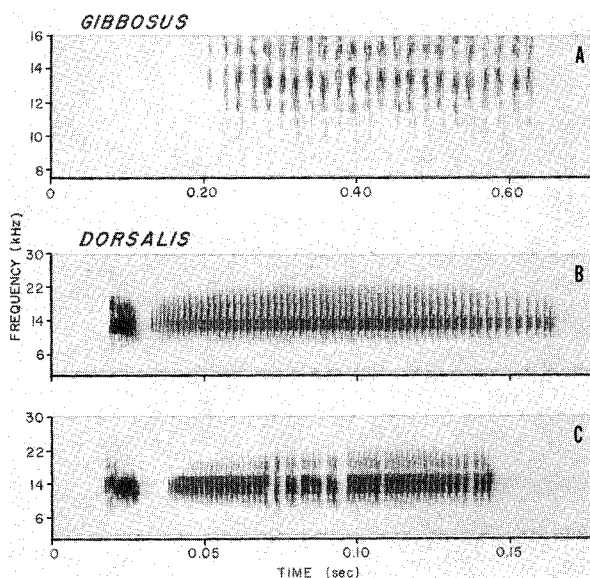


FIG. 1.—Audiospectrograms of *Atlanticus* songs at 23.5°C. A. *A. gibbosus*. One phrase consisting of 12 phonotomes. Each phonotome, except the first, consists of 2 major sounds (note the subtle pairing). The 2 major sounds of a pair are probably made in the manner that Pierce (1948) described for *A. testaceus*—i.e., each cycle of wing movement includes 2 acoustically effective closures separated by a partial opening. Phonotome rate in *A. gibbosus* was calculated using the second through final phonotome in a phrase. (Phrases are produced in groups of 2–4 at a rate of ca. 1 per second. The groups occur at irregular intervals.)

B, C.—*A. dorsalis*.—B, One phonotome, consisting of a brief initial sound (probably produced by a rapid opening movement) followed by a prolonged sound containing 59 tooth-strikes (probably produced by a slow closing movement). Both the sounds and the tegminal movements proposed as producing them are nearly identical to those of the ephippigerine katydid *Ephippiger bitterensis* Marqu. (Pasquinelli and Busnel 1954). Tooth-strike rate was calculated by dividing the duration of the prolonged sound by the number of tooth-strikes. (Phonotomes are produced in irregular groups at irregular intervals. Groups of 2 are frequent but have no apparent homology to the paired major sounds of *A. gibbosus*.) C, A typical phonotome produced by the same individual as in B but after 61 days of calling (see text). Missing tooth-strikes (7 in the above example) were added to the actual tooth-strikes (53) in calculating tooth-strike rate.

RESULTS AND DISCUSSION

Temperature.—The phonotome rate of *A. gibbosus* closely approximates a linear function of temperature (Fig. 2). Linear regression explains 99% of the variance in phonotome rates, and the error sum on squares ($\sum[y - \hat{y}]^2$) is 7.45. Most physiologists use Q_{10} values in describing effects of temperature on rates in poikilotherm nervous systems, yet such values are predicated on rates being exponential functions of temperature. If an exponential model is used to describe effects of temperature on *Atlanticus gibbosus* phonotome rate, the line of best fit is $\text{Ln } \hat{y} = 0.055 T + 1.786$ ($r^2 = .970$), and the error sum of squares becomes 37.52. Since the error sum of squares for the exponential model is 5 times that of the linear

model, the linear model is clearly superior. Similarly linear relationships of phonotome rate to temperature have been reported for crickets and for other species of katydids (Walker 1975) including one other decicline—*Atlanticus testaceus* (Scudder) (Dumortier 1963). The formula of an eye-fitted line for *A. testaceus* is $\hat{y} = 0.85 T - 5.22$.

In the katydid genus *Orchelimum* and in a variety of crickets, the regression lines for phonotome rate on temperature tend to converge at $\hat{y} = 0$ (Walker 1962, 1975). For *A. gibbosus* the value of T at $\hat{y} = 0$ is 7.1°C and for *A. testaceus* it is 6.1°C. Other species of *Atlanticus* may be expected to have similar values.

The tooth-strike rate in *A. dorsalis* is described approximately as well as a linear or as an exponential function of temperature (Fig. 3–4). The error sum of squares for the linear model is 176,063 and for the exponential model is 201,415.

In crickets, unlike tettigoniids, tooth-strike rate and carrier frequency coincide. Frequency is easily determined and the relationship of tooth-strike rate and temperature is known for more than 20 species of crickets representing 5 subfamilies (e.g., Walker 1962, 1969a,b). In none of the cricket species is the effect of temperature on tooth-strike rate like the effect in *A. dorsalis*. In crickets the increase in tooth-strike rate with increasing temperature either remains constant or decreases. In *A. dorsalis*, the increase in tooth-strike rate tends to be greater at higher temperatures (Fig. 3–4). I do not know the reason for this discrepancy nor whether other katydids are like *A. dorsalis*. In calling crickets, sound is made only on the closing stroke of the tegmina; therefore, in species

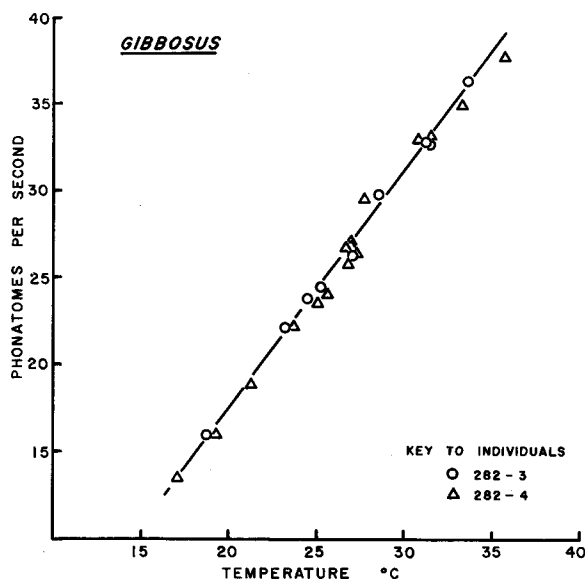


FIG. 2.—Effect of temperature on phonotome rate in 2 individuals of *Atlanticus gibbosus*. (Phonotome rate corresponds to wing-cycle rate.) Adult age was 42–54 days (since capture) for individual 282–3 and 20–46 days for 282–4. The line depicts the linear regression of phonotome rate on temperature: $\hat{y} = 1.35 T - 9.56$ ($r^2 = .992$).

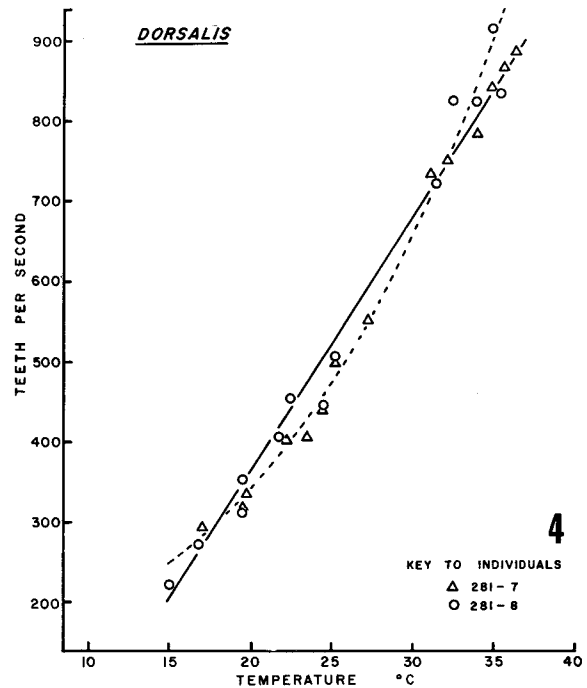
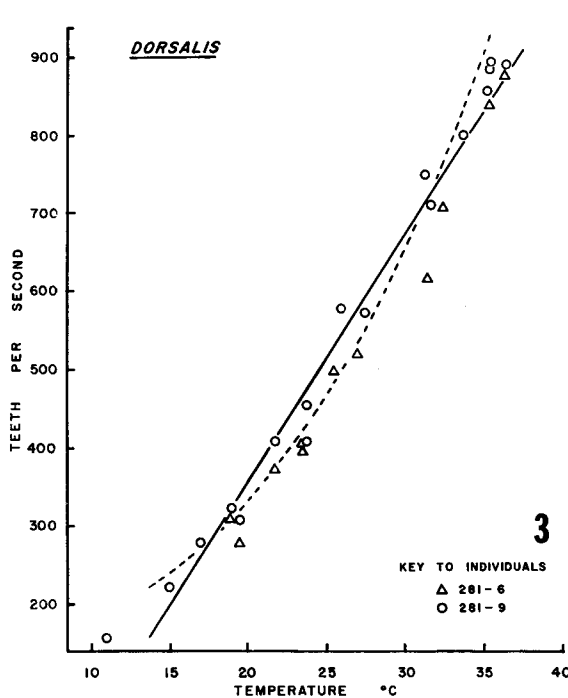


FIG. 3, 4.—Effect of temperature on tooth-strike rate in 4 individuals of *Atlanticus dorsalis*. Adult ages were 2–19 days (since capture) for all specimens. The lines depict linear and exponential regressions of tooth-strike rate on temperature for all tape recordings of *A. dorsalis* (84 tapes of 4 individuals, ages 2–77 days): $\hat{y} = 33.55 T - 268.32$ ($r^2 = .959$) and $\text{Ln } \hat{y} = .065 T + 4.523$ ($r^2 = .962$).

in which frequency shows a declining rate of increase at higher temperatures the wing speed on opening (the silent movement) must show an increasing rate of increase. If this seems strange, recall that wing-cycle rate is a linear function of temperature; consequently, the rate of movement for the opening and closing strokes combined must increase at a uniform rate with increasing temperature. One potential explanation for the relation in *A. dorsalis* is that the wing movements have the same temperature-related changes as in crickets but that sound is made on tegminal opening rather than on tegminal closing. Another is that coincidence of tooth-strike rate and carrier frequency in crickets places a restriction on the rate of increase that is absent in tettigoniids.

The value of T for $\hat{y} = 0$ in the linear model for *A. dorsalis* tooth-strike rate is 8.0°C —surprisingly close to the corresponding values for phonatome rate in *A. gibbosus* and in *A. testaceus*.

Humidity.—At 27°C the phonatome rates of *A. gibbosus* at 60% RH were not consistently lower than those at 95% RH, but at both 27 and 31°C the rates at 25% RH were consistently lower than those at 95% RH (Table 1). The average difference of the means for individuals at the two contrasting humidities was 0.9 phonatome/s. The regression formula for *A. gibbosus* reveals that such an effect is equivalent to that of a decrease in temperature of 0.7°C ($0.9/1.35$). Depression of body temperature to this extent as a result of transpiration is well known in insects (Bursell 1964), and I see no reason to attribute the

effect of humidity on stridulatory rate in *A. gibbosus* to any phenomenon that is more complicated. A similar decrease in stridulatory rates at low humidities occurs in crickets (Walker 1962). Under field conditions humidity effects should be of little significance because individuals generally sing only in microclimates with high humidities and because fluctuations in ambient temperature would easily obscure any humidity effects that did occur.

Age.—In *Drosophila melanogaster* Meigen, wing-beat frequency in flight increases by more than 10% as the adult ages (Chadwick 1953). I looked (1962) for an age effect in wingstroke rates in stridulating crickets but found none. However, Whitesell² found that older males of a coneheaded katydid, *Neoconocephalus triops* (L.), had significantly slower stridulatory wingstroke rates. After aging 42 days, 8 ♂ dropped in rate at 25°C from 101 to 94 wingstrokes/s. Whitesell also discovered that if adult males of *N. triops* diapaused, they subsequently had a slower phonatome rate and grouped their phonatomes differently.

Four *A. gibbosus* were repeatedly tape recorded on at least 2 occasions more than 3 wk apart (Table 2). For no individual were the mean pulse rates for any 2 such occasions significantly different. However, one individual (282-4, Table 2), taped 25 times during a period of 54 days, showed a slight, but statistically

²J. J. Whitesell. 1974. Geographical variation and dimorphisms in song, development, and color in a katydid: field and laboratory studies (Tettigoniidae, Orthoptera). Ph.D. dissertation, Univ. of Florida, Gainesville (Xerox Univ. Microfilms, Ann Arbor, Mich.). 75 pp.

Table 1.—Effect of humidity on wingstroke rate in *Atlantiscus gibbosus* at 2 ambient temperatures.

Individual ^a	Differences in average deviation from expected phonatome rate ^b :	
	$\bar{X}_{95\% RH}$	$-\bar{X}_{25\% RH}$ (phonatomes/s)
	27±0.5	31±0.5
282-4	—	1.5
282-6	0.7	—
282-7	1.0	1.6
282-8	0.9	0.7
282-10	—	0.5
282-11	—	0.6
282-12	—	0.3
Average differences ($\bar{X} \pm SD$)	0.9±0.2	0.9±0.5

^a Identifying numbers are those used in the Tape Library, Dept. of Entomology, Univ. Florida.

^b The regression formula was used to predict the phonatome rate for each tape recording. The deviations from expected were averaged for each humidity and temperature set point. The values in the table are differences between average deviations, i.e.,

$$\left(\frac{\sum(y - \hat{y})}{n} \right)_{95\% RH} - \left(\frac{\sum(y - \hat{y})}{n} \right)_{25\% RH} = \bar{X}_{95\% RH} - \bar{X}_{25\% RH}$$

significant, increase in phonatome rate. The rate of increase (.017 phonatomes/s/day) was so low that in 60 days (probably longer than ecological life expectancy) the phonatome rate would have increased by only 1.0 phonatomes/s—equivalent to an increase in ambient temperature of 0.8°C.

Three *A. dorsalis* were taped repeatedly during their first 3 wk of captivity and again after 4 more wk. One individual (281-8) produced such erratic phonatomes after the 7th wk that tooth-strike rate could not be determined. The other 2 were not so erratic and showed substantial increases in tooth-strike rates (Table 2). The effect is probably of no ecological importance because death comes sooner under field conditions. In the habitat where the experimental subjects were collected by their songs on 31 May, the first songs were heard in mid-April and the last were heard in mid-June. The recordings with significantly higher tooth-strike rates were made 21 July–17 August.

Yet another acoustical effect of old age was evident in *A. dorsalis*. After the 3 ♂ had sung for more than 50 days, the prolonged portions of their phonatomes had gaps that apparently corresponded to teeth missed by the advancing scraper (e.g., Fig. 1C). No tapes of these 3 specimens were made between 19 and 51 days of age; therefore, the ontogeny of the effect is unknown. From day 51 until their death all phonatomes they produced had the gaps. For each of the three specimens the number and positions of the gaps were distinctive. The files of 2 of the 3 ♂ were examined at 50× in hopes of finding worn or broken teeth at corresponding portions of the files. No local-

ized wear or damage was detected, but in both males the entire file appeared worn in comparison with the files of 2 specimens that had been killed immediately after being detected in the field by their songs. The number of teeth in the file, excluding the poorly formed teeth at either end, was in good agreement with the maximum number of tooth strikes in the prolonged portions of the phonatomes. For example, individual 281-6 (Fig. 1B, C) had 71 teeth in its file but only 63 well-developed ones. The number of tooth strikes in the prolonged portion of its phonatomes varied from 51 to 63.

Perhaps the most noteworthy aspect of the phonatomes of unnaturally old *A. dorsalis* is that the time required for missing a tooth is as great as the time required for striking one: the speed of wing movement seems independent of feedback from the mechanical shock and friction of tooth-strikes. In many katydids and crickets a similar phenomenon occurs for entire wing-cycles—i.e., gaps that occur erratically in phonatome sequences are usually of the same duration as a phonatome.

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Table 2.—Effect of age on stridulatory rates in *Atlantiscus* spp.

Species	Individual	Age (days) ^a	No. tapes	Deviations from expected rates ($\bar{X}_{y - \hat{y}} \pm SD$)	
				Linear model	Exponential model
<i>A. gibbosus</i> ^b	282-4 ^c	20-26	6	0.0±0.9	
		28-34	6	-0.3±0.3	(not applicable)
		46-48	9	0.3±0.6	
		72-73	4	0.6±0.4	
	282-6	3-5	10	0.7±0.3	
		29-30	4	-0.2±0.4	
	282-7	3-5	11	1.7±0.5	
		29-30	7	1.7±0.6	
282-8	3-5	6	1.4±0.5		
	29-30	8	1.9±0.8		
<i>A. dorsalis</i> ^d	281-6	2-19	11	-52±31	-46±45
		51-78	16	8±52	16±48
	281-7	2-19	14	-17±28	-19±41
		51-67	13	44±38	46±37

^a Number of days elapsed since adult was captured.

^b Many of these tapes were made during tests for effects of humidity; the ones that were made at 25% RH were treated as though made at 0.5°C less than ambient temperature (See Table 1 and text).

^c Regression of $\bar{X}_{y - \hat{y}}$ on age yields a slope of .017 (deviation per day of age) ($r^2 = 0.18$). The hypothesis that the slope is 0 is rejected at the $P = .05$ level.

^d A *t*-test of the differences between deviations of early and late songs of the 2 individuals showed a significant change with age ($P < .02$) whether the linear or exponential model used.

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