

# PHYSICAL CHARACTERISTICS OF THE DRUMMING OF *MECONEMA THALASSINUM*

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**Abstract**—The drumming sound of *Meconema thalassinum* (De Geer) (Orthoptera: Tettigoniidae: Meconematinae) was studied in a North American population. Males of *Meconema* produce sound by tapping one of their hind feet on the substrate. Each phrase consists of a variable number (0–5) of short impact trains (mean, 5.6 foot impacts per train), followed by 1–5 long impact trains (mean, 34.4 impacts). The most common type of phrase consists of 3 short and 2 long trains.

Foot impacts are produced at rates between 29 and 62/sec in the range 21.0–31.2°C. The foot–impact frequency follows a linear relationship with temperature; a similar relationship holds for the impact–train repetition rate, expressed as the reciprocal of the silent intervals between trains. The number of impacts per train and the overall phrase structure are essentially temperature-independent.

The drumming of *Meconema* is compared with the sounds produced by other Orthoptera, in terms of temperature dependence and of complexity of the phrase structure.

**Key Word Index:** *Meconema*, *M. thalassinum*, sound production, drumming, song structure, temperature dependence

## INTRODUCTION

*MECONEMA thalassinum* (De Geer) is a Palearctic katydid, known in England as the Oak Bush Cricket, that in recent years has become established in North America (GURNEY, 1960a, 1960b; JOHNSTONE, 1970; SISMONDO, 1978). The males do not have a conventional stridulatory apparatus, but both males and females have tegminal denticles (CAPPE DE BAILLON, 1921) similar to the sound-producing structures found in females of the Phaneropterinae: their function in *Meconema* is unknown. Males produce sound by tapping one of their hind feet on the substrate; this drumming has been described in the literature (CURRIE, 1953; RAGGE, 1965), but little of a quantitative nature has been published (RAGGE, 1973). The drumming of *Meconema* is a very unusual means of sound production among the Tettigoniidae: this report presents an analysis of its physical characteristics and some comparisons with the more conventional songs of related insects.

## MATERIALS AND METHODS

*M. thalassinum* adults were collected in Westchester County, New York, during late July and early August 1978 and 1979: both sexes were found after dark on the trunks of trees; out of several dozen specimens, all but four were on maples (*Acer* spp.), although oaks and other deciduous trees are common in the area.

Single males drum either in isolation or in the presence of females; groups of males caged together engage in drumming choruses, in which the phrases of different males alternate with little or no overlap: many of the recordings analyzed in this study were made during such group drumming. Drumming takes place after dusk, with or without room illumination; in

my experience, drumming is very rare at temperatures below 20°C.

Seven males were recorded on magnetic tape at 19 cm/sec (Grundig TK-340, GDM-310 microphone). The records were translated into photographic traces and analyzed using the apparatus and methods described elsewhere (SISMONDO, 1979). The impact frequencies were measured separately on every impact train of 79 phrases, and a weighted average frequency for each phrase was computed for use in the calculations and illustrations; a similar procedure was followed for the silent intervals between the impact trains of each phrase.

## RESULTS

During drumming, *M. thalassinum* males hold their wings elevated, extend the abdomen, and fold the tibia of one hind leg against the femur at an acute angle; the femur then vibrates over a small angle, causing the tarsus to strike the substrate. The abdomen also vibrates at a rapid rate, although it does not normally touch the substrate. During drumming, no motion of the head and thorax is visible, suggesting that the abdominal vibrations dynamically balance the femoral vibrations. One specimen, observed during many bouts of drumming, used either the left or the right hind leg indiscriminately.

Each drumming episode consists of an introductory series of short foot–impact trains (sometimes omitted), followed by a series of long trains (Fig. 1A). Table 1 shows the observed distribution of train patterns for 7 individuals. Figure 1B and Table 2 show the distribution of the number of impacts per train for the same population. The intervals between trains are relatively uniform over each phrase, but if there are

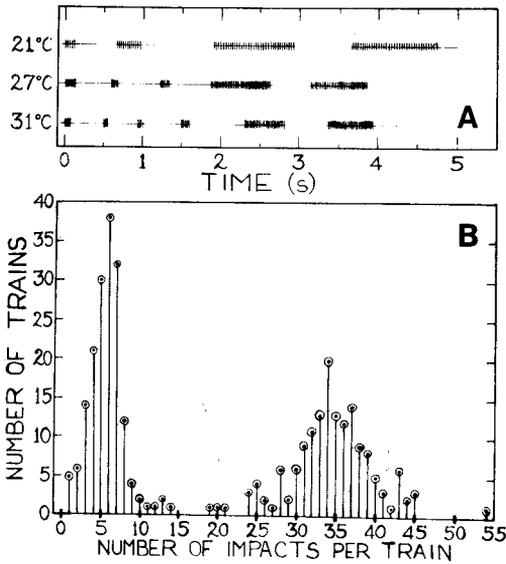


Fig. 1. Phrase structure in the drumming of *M. thalassinum*. (A) Three representative phrases (schematic) at different temperatures. (B) Number of impacts per train; the strongly bimodal distribution clearly supports the distinction between short trains and long trains.

more than 2 long trains the interval between the second and the third is apt to be considerably longer than the others.

The most common type of phrase consists of 3 short followed by 2 long trains; each male favours one type of phrase, e.g. 2-2 or 3-1, but can produce a variety of different types.

#### Temperature dependence

Figure 2 shows the behaviour of foot-impact frequency (femoral vibration rate) as a function of temperature. It is based on pooled data for 7 males; each point represents the weighted average frequency for all trains in one complete phrase. Each individual has a characteristic rate, some being slower or faster than others at all temperatures. The relationship is linear over the range studied (21.0–31.2°C), and is represented by the regression equation:

$$\text{Frequency (/sec)} = 2.10 T (^{\circ}\text{C}) - 8.23 \quad (r = 0.954)$$

Extrapolation of this equation to zero frequency gives a temperature of 3.9°C.

The reciprocal of the interval between onsets of successive pulse trains is not a good measure of train repetition frequency, because the duration of the train

Table 1. Distribution of different types of phrases, classified according to number of short and long impact trains. ( $n = 79$ , pooled data for 7 individuals).

Number of short impact trains	Number of long impact trains				
	1	2	3	4	5
0	—	7	—	—	—
1	6	9	2	1	—
2	7	10	2	—	1
3	3	14	4	2	—
4	—	9	1	—	—
5	—	—	1	—	—

Table 2. Mean number of impacts per train, as a function of position of each train in the phrase. All phrases were treated on a common basis by assigning No. 6 to the first long train, the only one found in every phrase; note that each phrase contains only a subset of all possible trains from 1 to 10, as seen in Table 1.

Train number	Number of phrases in which train is present	Mean number of foot impacts per train
1	1	4.0
2	11	3.73
3	33	4.97
4	53	4.76
5	71	6.90
6	78	34.43
7	61	34.93
8	14	33.49
9	4	27.75
10	1	33.0

included in each interval varies considerably during a phrase (Fig. 1A); a better measure of train repetition rate is the reciprocal of the silent interval between trains, which is reasonably consistent within each phrase. Figure 3 shows a plot of intertrain intervals against temperature; while there is a great deal of scatter in the data, temperature dependence is clearly evident. A least squares regression equation representing the data is:

$$\text{Reciprocal interval (/sec)} = 0.097 T (^{\circ}\text{C}) - 0.50 \quad (r = 0.559)$$

Note that the plot of this equation on Fig. 3 is curved, because the ordinate represents the silent interval itself rather than its reciprocal. When the equation is extrapolated to zero rate (i.e. infinite interval) the corresponding temperature is 5.2°C; this is in surprisingly good agreement with the temperature intercept for zero foot-impact frequency, considering

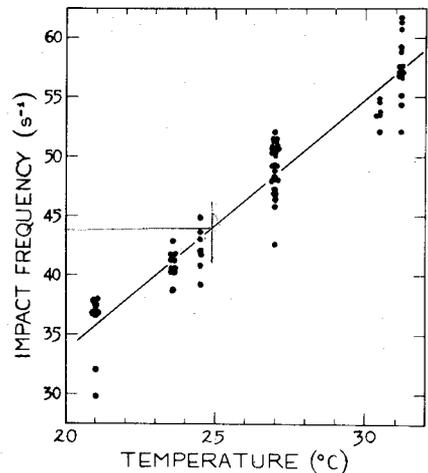


Fig. 2. Foot-impact frequency (= femoral vibration rate) as a function of temperature. Each point is the weighted mean frequency of all the trains in one complete phrase. The line represents the regression equation:

$$F(\text{/sec}) = 2.10 T (^{\circ}\text{C}) - 8.23$$

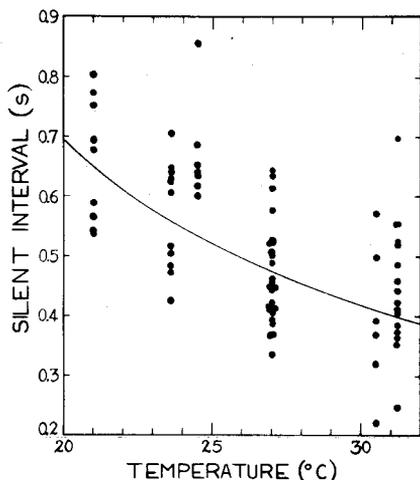


Fig. 3. Duration of silent intervals between pulse trains as a function of temperature. Each point is the mean of the durations of all silent intervals in one complete phrase. The curve is a plot of the regression equation:

$$T.R.F. (\text{sec}) = 0.097 T (^{\circ}\text{C}) - 0.50,$$

where *T.R.F.*, the train-repetition frequency, is equal to the reciprocal of the silent interval between trains.

the large standard error in the regression coefficient (0.017).

The number of impacts per train and the structure of the phrase appear to be unaffected by temperature variations; the only detectable effect is a slight increase in the proportion of phrases with more than 2 long trains at the higher temperatures. This may be a fortuitous result, reflecting contribution of different individuals to data at different temperatures.

## DISCUSSION

The two frequency-temperature equations obtained above, one for foot-impact frequency and one for train repetition rate, may be reduced to a comparable basis by computing a normalized temperature coefficient ( $C_n$ ) equal to the logarithmic derivative of frequency with respect to temperature. For a linear equation of the form:

$$F = aT + b \quad (F \text{ in } / \text{sec}, T \text{ in } ^{\circ}\text{C})$$

the temperature coefficient is:

$$C_n = \frac{1}{F} \left( \frac{dF}{dT} \right) = \frac{1}{(T + b/a)} \quad (^{\circ}\text{C}^{-1})$$

When the linear equation is extrapolated to zero frequency, the temperature equals  $-b/a$ : the term  $b/a$  also appears in the denominator of the expression for  $C_n$ . The temperature at zero rate has been shown by WALKER (1975a) to be a useful parameter in describing the temperature dependence of rates in the nervous systems of poikilotherms: if the dependence is linear, that parameter and the temperature coefficient are intimately related, as shown above.

The temperature coefficients of different activities of the same insect are not necessarily identical: for example, in the cricket *Oecanthus nigricornis* the wingstroke rate and the tooth-impact frequency

during stridulation obey different laws of temperature dependence (SISMONDO, 1979). In *Meconema*, values of  $C_n$  at 25°C, computed from the regression equations, are as follows: foot-impact rate, 0.0474/°C; train repetition rate, 0.0504/°C. These values are not significantly different, suggesting that the neural timing mechanisms involved in the control of foot-impact rate and of train-repetition rate obey the same underlying temperature response law. This conclusion is not very robust, in view of the large uncertainty in the regression coefficient for train repetition rate.

A consequence of these results is that for phrases of any given structure, the durations of the active and silent portions are in a ratio which is nearly invariant with temperature. For example, again on the basis of the regression equations, an increase of 10°C (from 21 to 31°C) shortens the silent intervals and the sound trains by very nearly the same factor (0.61 and 0.63 respectively, assuming equal number of foot-impacts at both temperatures).

## Comparisons with other Orthoptera

Sound production by femoral vibration is most unusual among Tettigoniids, but is common among the short-horned grasshoppers (Acrididae): in the latter, sound may be produced by impact on the substrate, or more commonly by the interaction between stridulatory organs on the femora and on the tegmina. In the Tettigoniidae, sound is normally produced by specialized stridulatory organs on the tegmina: as these are opened and closed, a scraper on the edge of the right tegmen strikes a row of teeth on a vein of the left tegmen. The temporal characteristics of Tettigoniid songs are determined both by wingstroke rate and tooth-impact frequency, while the acoustical properties depend in large part on the mechanical characteristics of the tegmina.

Each foot impact of *Meconema* involves one complete cycle of femoral motion: thus the impact frequency of *Meconema* is analogous, in a gross neuromuscular sense, with the wingstroke frequency of more conventional Tettigoniids. The foot-impact rate during drumming is comparable in magnitude with the wingstroke rates of Tettigoniids and Gryllids of similar size, and obeys similar linear laws of temperature dependence (WALKER, 1975a).

Many Tettigoniids with high wingstroke rates (e.g. Conocephalinae) produce phrases with a simple, repetitive temporal structure; in the Copiphorinae, the wingstroke rate is normally uniform, but motion within each wingstroke may involve complicated accelerations and decelerations (WALKER, 1975b); the most elaborate songs are found among the Phaneropterinae (WALKER and DEW, 1972), where the timing of the wingstrokes as well as the motions within each wingstroke may be very complex: in general, the phrases of species with the most complicated songs consist of only a few wingstrokes.

The drumming of *Meconema* consists of up to 150 foot impacts, divided into as many as 8 trains of two different types: thus, although *Meconema*'s drumming is very simple from the standpoints of fine motor control and acoustics, its temporal phrase structure places it among the more complex Tettigoniid sounds.

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