

Effects of Temperature on Rates  
in Poikilotherm Nervous Systems:  
Evidence from the Calling Songs of Meadow Katydid  
(Orthoptera: Tettigoniidae: *Orchelimum*)  
and Reanalysis of Published Data

Thomas J. Walker

Department of Entomology and Nematology, University of Florida,  
Gainesville, Florida, USA

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*Summary.* 1. Male calling songs of 10 species of *Orchelimum* were tape-recorded 9 to 52 times over ranges of ambient temperatures as great as 20 °C.

2. For each species the relation between wingstroke rate and temperature was approximately linear. Calculated regression lines had coefficients of determination ( $r^2$ ) between 0.76 and 0.99 (aver.  $r^2 = 0.93$ ). The slopes of the regression lines varied from 0.9 to 5.1, but when extrapolated downward to  $\hat{y} = 0$ , the lines tended to converge at 11 °C ( $\bar{x} \pm SD = 10.9 \pm 1.9$ ).

3. These results are similar to those published for 27 species of crickets and known for 20 additional species of katydids.

4. In previous studies, by others, the effects of temperature on rates within poikilotherm nervous systems have generally been reported as  $Q_{10}$  values. Such values are appropriate if rates approximate an exponential function of temperature. However, reanalysis of 15 published data sets that were adequate to justify a comparison showed that 13 fit a linear model more closely than an exponential one. Furthermore, if one half a data set was used to predict the other half, the linear model was superior to the exponential model 26 of 30 times. The temperature ranges of the 15 data sets were as small as 12 and great as 26 Celsius degrees.

5. For those 13 data sets with an  $r^2 > 0.90$ , the regression lines tended to converge like those of katydids and crickets. For seven species of electric fish the values of  $x$  when  $\hat{y}$  (discharge rate) = 0 clustered about 4 °C ( $\bar{x} \pm SD = 4.0 \pm 1.8$  C).

6. Empirically the linear model is superior to the exponential one in (1) goodness of fit, (2) prediction of effects beyond the temperature range studied, and (3) prediction of data sets from a single or no datum.

7. The origin and slope of the linear regression are generally more useful than  $Q_{10}$  values as short-hand expressions of temperature effects on rates in poikilotherm nervous systems.

8. Rates in poikilotherm nervous systems are more complex in their determinants than are rates of *in vitro* chemical reactions. It is therefore not surprising that the former rates fail to show the simple exponential relations to temperature that the latter show. On the other hand, that poikilotherm nervous systems should generally have approximately linear relations to temperature and that the extrapolations of linear regression lines should tend to converge at zero rate are unexpected and reveal a need for more study of underlying causes.

### Introduction

Surprisingly little is known of the effects of temperature on rates within poikilotherm nervous systems. Most studies have reported values at only two or a few temperatures and have dealt with one or a few species. The only generali-

zation that seems to have been made from the published data is that higher rates occur at higher temperatures and lower rates occur at lower ones.

The data reported here concern the effects of ambient temperatures upon wingstroke rate during calling of 10 species of meadow katydids (*Orchelimum*). These data and published and unpublished data on 47 other species of crickets and katydids (Gryllidae and Tettigoniidae) and published data on earthworms, crayfish, and electric fish conform to generalizations that may reflect previously unsuspected regularities in temperature effects on poikilotherm nervous systems.

### Materials and Methods

The procedures for studying *Orchelimum* wingstroke rate were similar to those used for crickets (Walker, 1962b). For the laboratory recordings, males of *Orchelimum* spp. were held individually in small cages in a controlled temperature room ( $\pm 0.5^\circ\text{C}$ ). They were exposed to the test temperature at least one hour before their songs were tape-recorded. Immediately after the song had been recorded, the temperature within the cage of that specimen was determined by inserting a thermocouple and reading the temperature with a potentiometer. Test temperatures extended above and below the range in which the caged individuals would sing. Humidity was not controlled, but tests with crickets (Walker, 1962b) and with katydids (Walker, 1975) indicated that humidity has little effect on wingstroke rates. Most of the tape recordings were made with an Ampex<sup>®</sup> 351 and are in the Tape Library of the Department of Entomology, University of Florida. The recordings of *O. vulgare* were made with a Magnecord<sup>®</sup> PT 63 and are in the Library of Animal Sounds, Ohio State University, Columbus. Some individuals were recorded in the field with a Kudelski Nagra<sup>®</sup> III recorder. The temperatures noted for field recordings are less accurate than those for laboratory recordings both because of the changeableness of field temperatures and the measurement of the temperature at the microphone rather than at the specimen.

Understanding the methods of analyzing the tape recordings depends on knowing the basic features of *Orchelimum* calling songs (Morris and Walker, 1975). Most species of *Orchelimum* have two techniques or modes of stridulating that they alternate during calling. In most such instances the two modes can be classified onomatopoeically as ticks and buzzes. In most species the wingstrokes are produced at irregular intervals during the ticking mode. In all species the wingstrokes are produced at regular intervals during the buzzing mode. With the exception of the "slow" wingstroke rate of *sylvaticum*, the wingstroke rates measured and discussed in this paper are those during the buzzing mode. In *militare*, the wingstrokes during the buzz are produced in trios and not only was the wingstroke rate within the trios calculated but also the trio rate.

The wingstroke rates of the recorded songs were determined from audiospectrograms made with a Kay<sup>®</sup> Sona-Graph and showing 1 or 2 sec of singing. The rate for each audiospectrogram was determined by counting the wingstrokes in the longest uniform series (usually  $> 25$  wingstrokes) and dividing by the duration. In *militare*, in which the longest uniform series was 3 wingstrokes, three series were counted and the three estimates of the rate were averaged.

A single audiospectrogram was found to give an adequate estimate of the wingstroke rate of a mode for an entire 20- to 30-sec tape recording. When audiospectrograms were made of different examples of the same mode within a tape recording (i.e. when 2 one- or two-sec samples were taken), the two calculated wingstroke rates seldom differed more than 2%. In *O. vulgare* (38 tapes), the coefficient of variation for measurements of different portions of the same tape recording was 0.7%.<sup>1</sup> In *O. pulchellum* (16 tapes) it was 0.08%!

<sup>1</sup> Where  $x_1$  = measurement of first portion of single tape,  $x_2$  = measurement of second portion,  $\bar{x}$  = mean of measurements of all tapes, and  $n$  = number of tapes,

$$\text{C.V.} = \frac{\sqrt{\sum(x_1 - x_2)^2 / 2n}}{\bar{x}} \times 100.$$

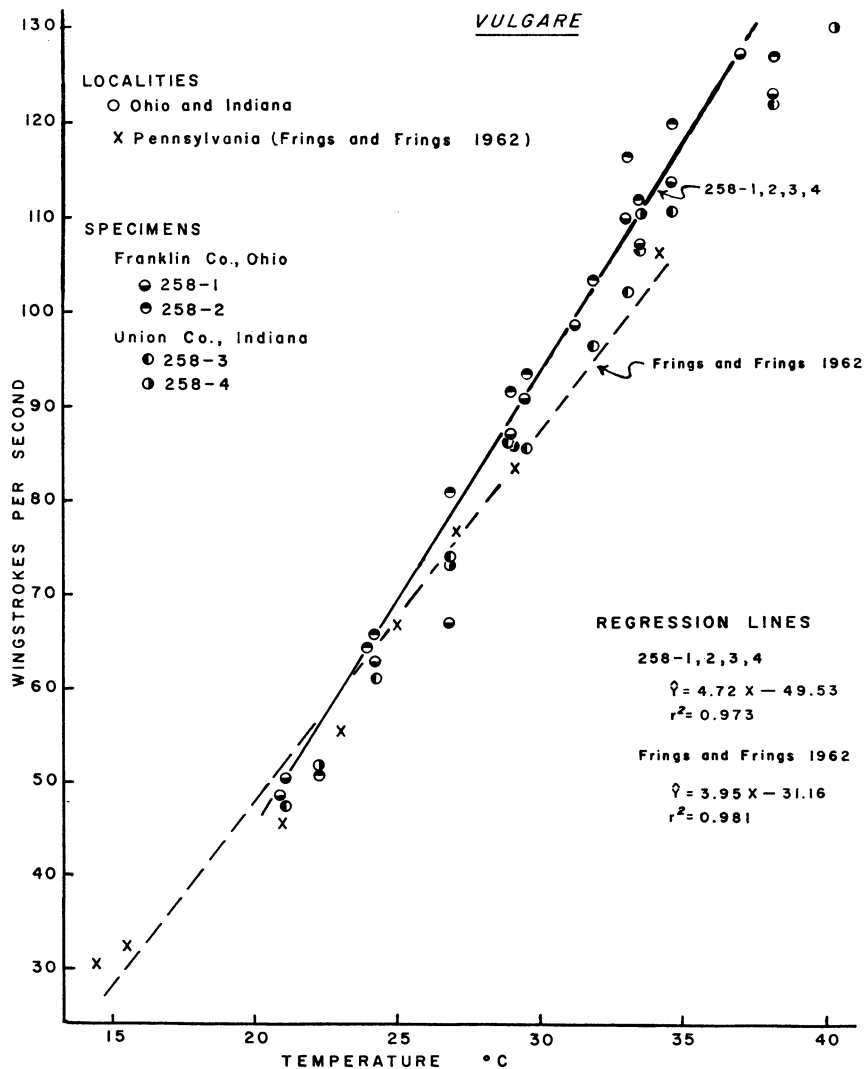


Fig. 1. Relation between ambient temperature and wingstroke rate during the buzzing mode of *O. vulgare*. Each point represents the mean of two analyses of different portions of a single laboratory-made tape recording. The data from Frings and Frings (1962: Table 2) are from two individuals but only one was reported at each temperature

### Results

Three generalizations concerning the data (Table 1, Figs. 1-4) seem tenable: (1) Wingstroke rate is an approximately linear function of temperature. This is evident by inspection for the six species for which all data are shown graphically (Figs. 1-4), and the linear regressions for the other four species had similarly high coefficients of determination (Table 1). (2) The greater the wingstroke rate

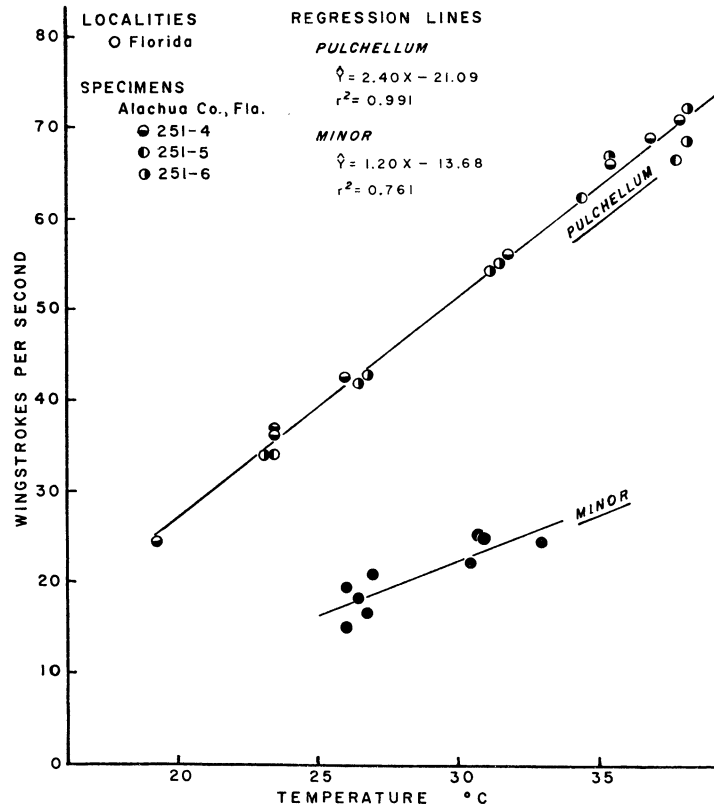


Fig. 2. Relation between ambient temperature and wingstroke rate during the buzzing mode of *O. pulchellum* and during the only type of wing movement made by *O. minor*. All tape recordings were made in the laboratory, and each is represented by a single point. For *pulchellum* each point is the mean of two analyses

at a given temperature, the greater is the change in wingstroke rate per unit change of temperature (i.e.  $b$  in the regression formula is greater). The order of the lines in Table 1 is based on the expected wingstroke rate at 30 °C ( $W_{30}$ ) and without exception the magnitude of  $b$  increases with each successive increase in  $W_{30}$ . (3) If the calculated regression lines are extrapolated downward to  $\hat{y} = 0$ , they tend to converge at 11 °C (Table 1, last column,  $\bar{X} \pm SD = 10.9 \pm 1.9$ ). In other words, if the wingstroke rate at a single temperature is known, the line describing temperature effects can be predicted by connecting that point with  $y = 0$  at 10.9 °C. The convergence of the regression lines can also be described in terms of their slopes ( $b$ ) being a linear function of  $W_{30}$ . For the 11 formulas for wingstroke rates in Table 1,  $\hat{b} = 0.0349 + 0.0517 W_{30}$ , with  $r^2 = 0.969$ . If one assumes that the intercept should be 0 (i.e. that  $b$  should be 0 when  $W_{30} = 0$ ), the formula for  $b$  becomes  $\hat{b} = 0.0524 W_{30}$ . The error sum of squares of this formula is less than 1% greater than that of the regression formula.

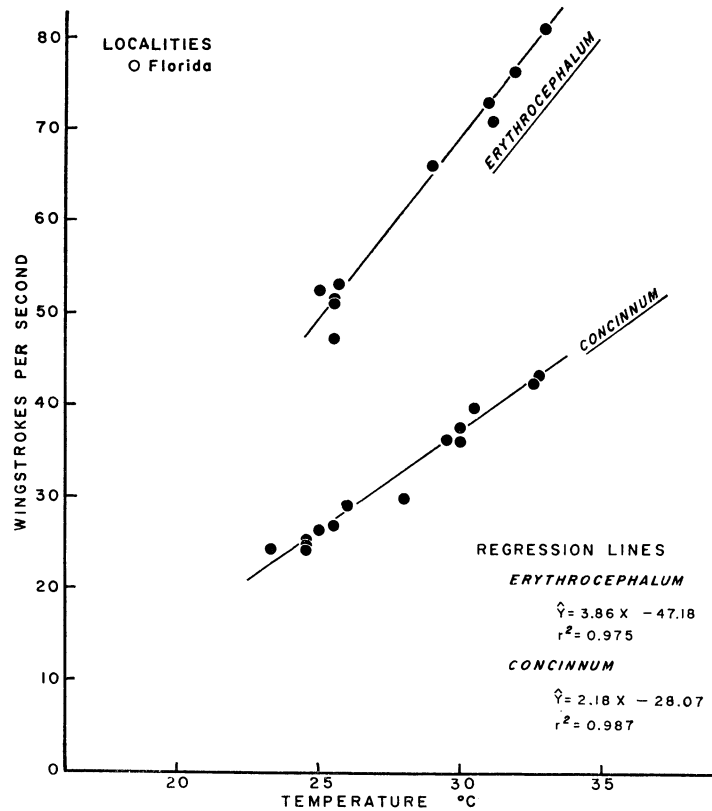


Fig. 3. Relation between ambient temperature and wingstroke rate during the buzzing mode of *O. erythrocephalum* and *O. concinnum*. All tape recordings were made in the laboratory, and each is represented by a single point

## Discussion

### *Katydid and Crickets*

Previously published studies of katydids and crickets are compatible with the present data and generalizations concerning effects of temperature on *Orchelimum* wingstroke rates. Frings and Frings (1962), in their study of *Orchelimum vulgare*, did not plot wingstroke rate during the buzzing mode against temperature, but they included the necessary data in a table. Their data are in good agreement with mine (Fig. 1): A linear regression of wingstroke rate on temperature accounts for 98.1% of the variance in their data ( $r^2 = 0.981$ ), and the temperature at  $\hat{y} = 0$  is 7.9 °C.

I have published data on the effects of temperature on the stridulation of 27 species of crickets in 5 subfamilies (Walker, 1962 a, 1962 b, 1963, 1969 a, 1969 b). The generalizations from the cricket data are identical to the ones for *Orchelimum* except that in crickets the temperatures at  $\hat{y} = 0$  cluster about a lower mean. In the original study (Walker, 1962 b) 19 species representing 5 subfamilies had

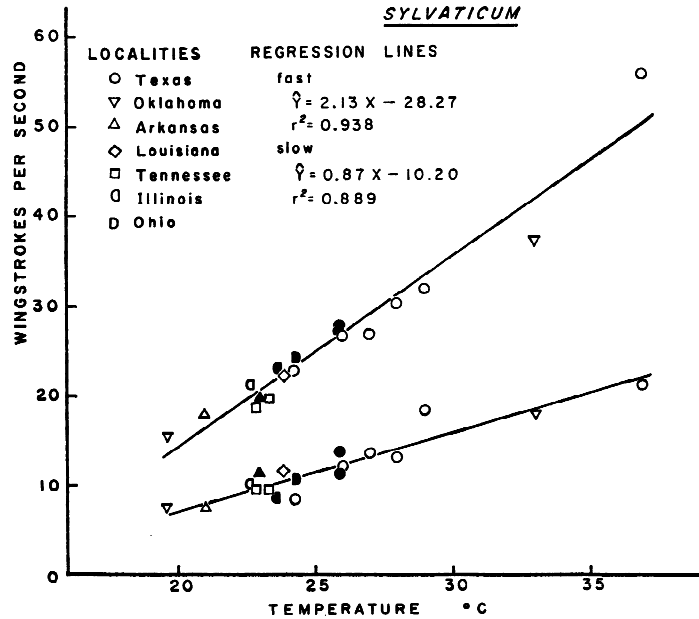


Fig. 4. Relation between ambient temperature and wingstroke rate during the calling song of *O. sylvaticum*. Each tape recording is represented by two points—one for the initial, slow type of wing movement and the other for the final, fast type of wing movement. Solid symbols are for laboratory-made tapes and open symbols are for field-made tapes

Table 1. Effects of temperature on wingstroke rate during calling in ten species of *Orchelimum* and on trio rate in *O. militare*

Species <sup>a</sup>	No. indiv.	No. tapes <sup>b</sup>	Range (°C) <sup>c</sup>	Regression line ( $\hat{y} = a + b(x)$ )	Coef. of det. ( $r^2$ )	$x$ when $\hat{y} = 0$ ( $-a/b$ )
<i>sylvaticum</i> (slow) (Fig. 4)	18	18 (13)	20-37	-10.20 + 0.87	0.889	11.7
<i>minor</i> (Fig. 2)	4	9	26-33	-13.68 + 1.20	0.761	11.4
<i>fidicinium</i>	22	28 (5)	20-33	-10.23 + 1.46	0.895	7.0
<i>sylvaticum</i> (fast) (Fig. 4)	18	18 (13)	20-37	-28.27 + 2.13	0.938	13.3
<i>concinnum</i> (Fig. 3)	11	15	23-33	-28.07 + 2.18	0.987	12.9
<i>pulchellum</i> (Fig. 2)	3	19	19-38	-21.09 + 2.40	0.991	8.8
<i>nigripes</i>	10	10 (6)	20-29	-23.69 + 2.52	0.932	9.4
<i>militare</i>	3	10	24-36	-32.44 + 2.93	0.898	11.1
<i>agile</i>	28	52 (2)	24-38	-35.08 + 3.16	0.963	11.1
<i>erythrocephatum</i> (Fig. 3)	6	10	25-33	-47.18 + 3.86	0.975	12.2
<i>vulgare</i> (Fig. 1)	4	38	21-40	-49.53 + 4.72	0.973	10.5
<i>militare</i> (trios)	3	10	24-36	- 9.01 + 0.82	0.932	11.0

<sup>a</sup> Localities for six species are given in Figs. 1-4. Localities for other species are as follows: *agile*, Florida, Georgia, Mississippi, Alabama, Maryland; *militare*, Florida; *nigripes*, Texas, Louisiana, Mississippi, Tennessee, Ohio; *fidicinium*, Florida, Georgia, New Jersey.

<sup>b</sup> In all but five instances, only tapes made under controlled temperatures in the laboratory were used. In these five instances, the number in parentheses gives the number of field tapes included in the total.

<sup>c</sup> Temperatures here rounded to nearest 1°. More exact temperatures used in calculations.

a value at  $\hat{y}=0$  of  $4.1 \pm 1.8$  °C ( $\bar{X} \pm \text{SD}$ ). In later studies of 8 more species (Walker, 1969a, 1969b), the same trends were repeated except that 6 species of *Orocharis* (Eneopterinae) had a value at  $\hat{y}=0$  of  $-1.0 \pm 3.0$  °C. None of these 27 species of crickets had a value at  $\hat{y}=0$  as high as the average for the 10 species of *Orchelimum* reported here.

I have data for 20 other species of katydids comparable to the data for the 10 species of *Orchelimum*. In every case the data indicate that wingstroke rate is a linear function of temperature. The figures in parentheses are for  $x$  at  $\hat{y}=0$ . Those expressed to 0.1 °C are from calculated regression lines; the rest are from eye-fitted lines. Four subfamilies are represented: Conocephalinae: *Conocephalus brevipennis* (10 °C), *C. fasciatus* (11 °), *C. nigropleuroides* (8 °), *C. strictus* (12 °), *Odontoxiphidium apterum* (9 °). Copiphorinae: *Belocephalus davisii* (7 °), *Bucrates malivolans* (6 °), *Neoconocephalus bivocatus* (3.6 °, Walker, Whitesell and Alexander, 1973), *N. ensiger* (6 °), *N. exiliscanorus* (7 °), *N. retusus* (4 °), *N. robustus* ( $-11.9$  °, Walker, Whitesell and Alexander, 1973). Decticinae: *Atlanticus gibbosus* (7.1 °, Walker, 1975), *A. testaceus* (6 °, Dumortier, 1963). Phaneropterinae: *Amblycorypha rotundifolia* (7 °), *A. floridana* (7 °), *A. sp. nr. uhleri* (8 °), *A. sp. nr. uhleri* (10 °), *Scudderia curvicauda* (8 °), *Scudderia texensis* (4.9 ° and 7.7 ° for fast and slow songs respectively, Spooner, 1964).

These data suggest that other genera of Conocephalinae are similar to *Orchelimum* in effects of temperature on calling songs and that except for some species of *Neoconocephalus* other subfamilies of Tettigoniidae are intermediate between Gryllidae and Conocephalinae as to their values for  $x$  at  $\hat{y}=0$ . The most non-conforming species listed is *Neoconocephalus robustus* ( $-11.9$  °C), which is also the species with the highest wingstroke rate (224/sec at 30 °C) and the only species in the above list known to maintain a significantly elevated thoracic temperature during calling (up to 15 °C above ambient). Of special importance in accounting for the atypical value for  $x$  at  $\hat{y}=0$  is the fact that the extent to which thoracic temperature is elevated above ambient decreases with increasing ambient temperature (Heath and Josephson, 1970). At 20 °C ambient the thoracic temperature averages 31 °, while at 30 °C it averages 37 °C. The degree of heating varies widely at a given ambient temperature (Heath and Josephson, 1970), and this is reflected behaviorally in the lowest coefficient of determination of the regression line of wingstroke rate on temperature ( $r^2=0.52$ , Walker, Whitesell and Alexander, 1973). *N. bivocatus* and *N. retusus* also have rapid wingstroke rates (150 and 170 closures per sec respectively at 25 °C), thus their relatively low values of  $x$  at  $\hat{y}=0$  may be caused by thoracic heating.

#### Other Poikilotherms

In reviewing previous reports of temperature effects on rates in poikilotherm nervous systems, I discovered that other workers seldom noted linearity and never convergence. Temperature effects were reduced to  $Q_{10}$  values, implying that rate was an exponential function of temperature. To determine whether singing rates in crickets and katydids were exceptional in their relation to temperature, I undertook to test previously published data against both linear and exponential models. Unfortunately, in most of the literature reviewed, the data

were from a few temperatures in a narrow range and were highly variable at a given temperature. Little could be gained by comparing the fit of such data to linear and exponential models. In the following instances, however, the published data seemed precise and extensive enough to be of value in comparing the two models: Lagerspetz and Talo (1967, Table 1) reported conduction velocities at 6 ° to 32 °C in the median and lateral giant fibers of the earthworm, *Lumbricus terrestris*, acclimated to 13 ° and 23 °C. They reported  $Q_{10}$  values of 1.45 to 3.12 depending on the temperature range and the particular fibers tested. Burkhardt (1959, Fig. 3) plotted the stationary discharge frequency of stretch receptors of *Astacus leptodactylus* (a crayfish) as a function of temperature. Hysteresis conspicuously lessened the precision of the data. Guttman and Barnhill (1970, Fig. 3) plotted period of repetitive firing of space-clamped axons of *Loligo pealei* (a squid) as a function of temperature. They adjusted the data for individual fibers "up or down by an average of 13.6% of the mean value for best fit"; consequently the precision of their data cannot be quantified. In making the calculations reported below, I used the reciprocals of estimated adjusted mean values for 5, 10, 15, 20, and 25 °C. Enger and Szabo (1968, Fig. 1) and Schwassmann (1971, Fig. 9) reported the discharge rates of electric organs of nine species of electric fish (representing 8 genera, see Table 2) as exponential functions of temperature. Only the electric fish data approach the precision and extensiveness of those for stridulatory wingstroke rates in katydids and crickets.

The 15 data sets from the studies cited above and 5 representative data sets from katydids were fitted to both linear and exponential models by standard statistical procedures. For all but three of the 20 data sets both linear and exponential models had  $r^2 \geq 0.90$ —i.e., at least 90% of the total variances (linear and logarithmic) was accounted for by the regression formula. The two models were compared for goodness of fit by summing the squares of the arithmetic deviations of the actual data points from the regression lines (Table 2). For 18 of the 20 data sets, the linear model provided a closer fit than the exponential. In the 2 instances that the exponential model was superior (discharge rate of *G. carapo* and firing rate of clamped squid axon), the ratios of the larger error sum of squares to the smaller were 1.2 and 1.6. On the other hand, in the 18 instances that the linear model was superior, the ratios varied from 1.1 to 15.9 with all but 8 values higher than 1.6 and with a median value of 2.6. If the 5 katydid data sets are excluded, the linear model was better than the exponential for 13 of the 15 remaining data sets and the ratios favoring the linear model had a median of 2.4.

Another, perhaps more powerful, comparison of the two models was based on the degree to which each model predicted one half of a data set from the other half. Each data set was divided into an upper and lower half on the basis of temperature, and both linear and exponential models were used to fit lines to both halves. The four lines were extrapolated and the fit of the points not used to calculate the particular line was computed by summing the squares of arithmetic deviations (Table 3). Once again the linear model was superior to the exponential one in most instances: 26 out of the 30 cases other than katydids. In this comparison the superiority of the linear model was as great as 83.6, and the ratios favoring the linear model had a median of 4.0. The maximum superiority for the exponential model was 50.2 and the median for the 4 cases was 2.8. I infer



Table 2. Goodness of fit of linear and exponential regression for published data sets describing effects of temperature on rates in poikilotherm nervous systems

Kind of data Source of data Data set	Error sums of squares <sup>a</sup>		Model giving best fit	Ratio <sup>b</sup>
	Linear model ( $\hat{y}_l = a + b_l x$ )	Exponential model ( $\hat{y}_e = b_e k^x$ )		
Stridulatory wingstroke rates in katydids (representative species)				
This paper				
<i>Orchelimum vulgare</i> (Fig. 1)	601	1966	linear	3.3
<i>Orchelimum pulchellum</i> (Fig. 2)	3597	12323	linear	3.4
<i>Orchelimum concinnum</i> (Fig. 3)	9.17	10.59	linear	1.2
<i>Orchelimum minor</i> (Fig. 2)	25.93	28.27	(linear) <sup>c</sup>	1.1
Walker 1975				
<i>Atlanticus gibbosus</i>	7.45	37.52	linear	5.0
Electric organ discharge rate in fish				
Enger and Szabo (1968) <sup>d</sup>				
<i>Steatogenys</i> sp.	127.7	195.9	linear	1.5
<i>Sternopygus</i> sp.	1169	1267	(linear) <sup>c</sup>	1.1
<i>Eigenmannia</i> sp.	2183	5985	linear	2.7
<i>Sternoramphus</i> sp.	3066	9105	linear	3.0
<i>Sternarchus</i> sp.	13665	37338	linear	2.7
<i>Sternarchorhynchus</i> sp.	7111	7677	linear	1.1
Schwassmann (1971) <sup>e</sup>				
<i>Gymnotus carapo</i>	52.50	42.69	exponential	1.2
<i>Sternarchus leptorhynchus</i>	1375	3329	linear	2.4
<i>Gymnorhamphichthys hypostomus</i>	128.7	167.3	(linear) <sup>c</sup>	1.3
Conduction velocity in earthworm				
Lagerspetz and Talo (1967)				
Median fiber, 23 °C acclimation	1.12	17.84	linear	15.9
Median fiber, 13 °C acclimation	1.813	2.517	linear	1.4
Lateral fiber, 23 °C acclimation	1.586	6.334	linear	4.0
Lateral fiber, 13 °C acclimation	0.495	2.517	linear	5.1
Stationary discharge rate in crayfish				
Burkhardt (1959)				
Stretch receptor	21.85	28.00	linear	1.3
Firing rate in squid				
Guttman and Barnhill (1970)				
Clamped axon	2844	1731	exponential	1.6

<sup>a</sup> Error sums of squares =  $\Sigma(\hat{y} - y)^2$ . For calculations involving the exponential model, logarithmic values of  $\hat{y}_e$  were converted to arithmetic values. The standard procedure of least squares applied to the linear model obtains  $\hat{y}_l = a + b_l x$  and minimizes the error sum of squares,  $\Sigma(y - \hat{y}_l)^2$ . Applied to the exponential model it obtains  $\hat{y}_e = b_e k^x$  and minimizes  $\Sigma(\log y - \log \hat{y}_e)^2$ . Comparisons in this paper are between  $\Sigma(y - \hat{y}_l)^2$  and  $\Sigma(y - \hat{y}_e)^2$ . It is recognized that  $\Sigma(y - \hat{y}_l)^2$  is not the minimum for all possible exponential curves. However, the standard procedure for fitting an exponential curve is to minimize  $\Sigma(\log y - \log \hat{y}_e)^2$ ; therefore, the quantity  $\Sigma(y - \hat{y}_e)^2$  seems the appropriate value to compare with  $\Sigma(y - \hat{y}_l)^2$ . As a test, five data sets were compared as to  $\Sigma(\log y - \log \hat{y}_l)^2$  and  $\Sigma(\log y - \log \hat{y}_e)^2$ . The results were similar to those of the reverse comparison in both sign and magnitude of ratios.

<sup>b</sup> The ratio is obtained by dividing the larger sum of squares by the smaller sum of squares. A ratio of 3.0 means that the better model was 3 times as effective in minimizing the error sum of squares.

<sup>c</sup> Parentheses call attention to the fact that neither the linear nor the exponential model explained 90% of the total variance—i.e. for neither model was  $r^2 \geq 0.90$ .

<sup>d</sup> The data used in calculations were read from an enlargement of the published figure.

<sup>e</sup> The data used in calculations were the original data, supplied by Schwassmann (personal communication, 1974).

Table 3. Comparison of linear and exponential models as predictors of rates above and below the range of temperatures of the observations. Each data set was divided on the basis of temperatures into upper and lower halves; each half was then used to predict the other

Data set <sup>a</sup>	Lower data used to predict upper <sup>b</sup>			Upper data used to predict lower <sup>b</sup>		
	Range (°C) <sup>c</sup>	Best model <sup>d</sup>	Ratio <sup>e</sup>	Range (°C) <sup>c</sup>	Best model <sup>d</sup>	Ratio <sup>e</sup>
<b>Katydids</b>						
<i>O. vulgare</i>	21–30	linear	24.7	30–40	linear	2.1
<i>O. pulchellum</i>	19–31	linear	61.4	32–38	linear	5.0
<i>A. gibbosus</i>	17–26	linear	29.0	27–36	linear	9.6
<b>Electric fish</b>						
<i>Steatogenys</i> sp.	20–31	linear	11.1	31–38	<i>exponential</i>	1.3
<i>Sternopygus</i> sp.	19–25	linear	2.3	25–36	linear	1.0
<i>Eigenmannia</i> sp.	21–26	linear	7.9	27–36	linear	3.2
<i>Sternoramphus</i> sp.	22–29	linear	14.8	29–38	linear	8.9
<i>Sternarchus</i> sp.	20–29	linear	11.0	30–39	linear	2.7
<i>Sternarchorhynchus</i> sp.	24–30	linear	3.3	31–39	linear	1.4
<i>G. carapo</i>	20–26	<i>exponential</i>	3.2	26–33	linear	1.5
<i>S. leptorhynchus</i>	20–26	linear	32.1	26–33	linear	6.1
<i>G. hypostomus</i>	23–29	linear	4.6	29–35	linear	1.0
<b>Earthworm</b>						
Median fiber, 23 AT	6–24	linear	83.6	24–32	linear	3.1
Median fiber, 13 AT	6–22	linear	32.1	22–32	linear	2.5
Lateral fiber, 23 AT	6–24	linear	13.2	24–32	linear	1.6
Lateral fiber, 13 AT	6–22	linear	17.7	22–32	linear	3.1
<b>Crayfish</b>						
Stretch receptor	5–13	linear	34.8	16–27	<i>exponential</i>	2.5
<b>Squid</b>						
Clamped axon	5–15	linear	1.5	15–25	<i>exponential</i>	50.2

<sup>a</sup> See Table 2 for kinds and sources of data and full names of species.

<sup>b</sup> If the data set had an odd number of points, the central point was assigned to “upper data”. The earthworm and squid data sets had only five points, and the central point was assigned to “lower data” as well as to “upper data”.

<sup>c</sup> Temperatures here rounded to nearest 1°. More exact temperatures used in calculations.

<sup>d</sup> The best model is the one with the smallest sum of squares of the arithmetic deviations of the unused data points from the extrapolated regression line. (For the exponential model the logarithmic deviations were converted to arithmetic deviations prior to squaring).

<sup>e</sup> The ratio was obtained by dividing the larger sum of squares by the smaller sum of squares. A ratio of 20.0 means that the better model was 20 times as effective in minimizing the sum of squares of the deviations from the extrapolated line—i.e. it was 20 times better as a predictor of the unused data.

from this analysis that rates either above or below those actually observed should be estimated more accurately if a linear rather than an exponential model is used.

One of the advantages of the linear model for the katydid and cricket data was that it revealed convergences permitting prediction of rates at all temperatures on the basis of the rate at a single temperature. Furthermore, it suggested that regression lines for yet unstudied katydids and crickets should conform to simple formulas (e.g.,  $-a/b = 11$  for meadow katydids). The same tendency toward

Table 4. Effects of temperature on poikilotherm nervous systems—linear regressions of previously published data

Data set <sup>a</sup>	No. data points	Range (°C) <sup>b</sup>	Regression line ( $\hat{y} = a + b(x)$ )	Coef. of det. ( $r^2$ )	$x$ when $\hat{y} = 0$ ( $-a/b$ )
<b>Electric fish</b>					
<i>Steatogenys</i> sp.	23	20–38	$-28.20 + 3.60x$	0.982	7.8
<i>Sternopygus</i> sp.	14	19–36	$73.26 + 1.69x$	0.497	( $-43.3$ ) <sup>c</sup>
<i>Eigenmannia</i> sp.	10	21–36	$-75.05 + 25.62x$	0.985	2.9
<i>Sternoramphus</i> sp.	18	22–38	$-99.79 + 38.55x$	0.995	2.6
<i>Sternarchus</i> sp.	20	20–39	$-149.10 + 46.53x$	0.989	3.2
<i>Sternarchorhynchus</i> sp.	19	24–39	$-171.00 + 61.03x$	0.994	2.8
<i>G. carapo</i>	18 <sup>d</sup>	20–33	$-10.98 + 2.30x$	0.961	4.8
<i>S. leptorhynchus</i>	28 <sup>d</sup>	20–33	$-109.83 + 27.21x$	0.996	4.0
<i>G. hypostomus</i>	26 <sup>d</sup>	23–35	$-8.69 + 1.08x$	0.764	(8.0) <sup>c</sup>
<b>Earthworm</b>					
Median fiber, 23 AT	5	6–32	$-0.16 + 0.64x$	0.994	0.2
Median fiber, 13 AT	5	6–32	$2.94 + 0.57x$	0.988	$-5.2$
Lateral fiber, 23 AT	5	6–32	$0.75 + 0.32x$	0.967	$-2.3$
Lateral fiber, 13 AT	5	6–32	$2.00 + 0.31x$	0.989	$-6.5$
<b>Crayfish</b>					
Stretch receptor	13	5–27	$-0.24 + 0.64x$	0.905	0.4
<b>Squid</b>					
Clamped axon	5	5–25	$-68.17 + 16.71x$	0.961	4.1

<sup>a</sup> See Table 2 for kind and source of data.

<sup>b</sup> Temperatures here rounded to nearest 1°. More exact temperatures used in calculations.

<sup>c</sup> Value omitted in further calculations since  $r^2$  for both exponential and linear models  $< 0.77$ . If only the 9 data points for *Sternopygus* sp. that are for temperatures less than 28°C are used, the regression line is  $\hat{y} = -12.02 + 5.48x$  ( $r^2 = 0.975$ ) and  $x$  when  $\hat{y} = 0$  is 2.2°C.

<sup>d</sup> The data used in calculations were the original data (as supplied by H. Schwassmann, personal communication, 1974).

convergence is evident for other poikilotherms (Table 4). The most extensive data are for electric fish. For the 7 species with  $r^2 > 0.90$ , the temperatures at  $\hat{y} = 0$  are  $4.0 \pm 1.8$  °C ( $\bar{x} \pm SD$ ) (range: 2.6° to 7.8°). For the 4 earthworm fibers the temperatures at  $\hat{y} = 0$  are  $-3.4 \pm 3.0$  ° (range:  $-6.5$ ° to 0.2°). These values and the ones for squid and crayfish are similar to those reported above for katydids and crickets.<sup>2</sup>

For previously published studies of temperature effects on the nervous systems of other poikilotherms the linear model has the same advantages over the exponential one as it has for studies of katydids and crickets: (1) observed points fit more closely, (2) unobserved points outside the temperature range studied are more accurately predicted, and (3) data sets can be predicted from single points

<sup>2</sup> Exponential functions have no property corresponding to the convergence of linear functions at  $\hat{y} = 0$ . Translating linear functions to  $Q_{10}$  values results in  $Q_{10}$  values that decrease as the inverse of the temperature. Furthermore for linear functions that converge at some value of  $x$  at  $\hat{y} = 0$ ,  $Q_{10}$  values for any particular temperature interval are identical. For example if the *Orchelimum* data are expressed as  $Q_{10}$  values, the  $Q_{10}$  for 20–21 °C approximates 2.6; for 25–26 °C,  $Q_{10} \simeq 1.9$ ; for 30–31 °C,  $Q_{10} \simeq 1.6$ .

(or, for that matter, as for the yet unstudied katydids discussed above, from no data at all).

The weakest aspect of the linear model is its lack of a theoretical basis. However, the exponential model—as applied to rates in poikilotherm nervous systems—is also deficient theoretically. There is a theoretical basis for applying the exponential model to *in vitro* chemical reactions, but rates in poikilotherm nervous systems are more complex in their determination. They involve, for instance, chemical reactions occurring across cell membranes, the propagation of such reactions along nerve fibers, and a variety of chemical and physical phenomena at synapses. More study of the components of fundamental neural processes and temperature effects thereon are needed before any model can be accepted for theoretical reasons. It will be surprising if any simple model is generally applicable. In the meanwhile the linear model has proved more heuristic than the exponential. The origin and slope of the linear regression are generally more useful than  $Q_{10}$  values as shorthand expressions of temperature effects on rates in poikilotherm nervous systems.

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Dr. Thomas J. Walker  
Department of Entomology and Nematology  
University of Florida  
Gainesville, Florida 32611, USA