

## TEMPERATURE, INCUBATION RATES AND ORIGINS OF DRAGONFLIES

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The slope value (b) of the power equation ( $\ln D = \ln a + b \ln T$ ) relating degree-days required for development (D) to temperature (T) in insects is a composite measure of temperature adaptation that is of higher negative value in warm-adapted species than in cold-adapted species. Temperate-zone dragonflies for which data are available have high negative slope values in the egg stage. This contrasts with temperate-zone stoneflies, which probably evolved in cold-temperate regions and are uniformly cold-adapted, and with temperate-zone mosquitoes, whose slope values decrease as species range further north. Temperate-zone Odonata appear, therefore, to have retained the characteristics of their tropical ancestors.

### INTRODUCTION

Our interest in life-history patterns of north temperate-zone insects has led us to explore adaptations to prevailing temperature regimes. We have developed the working hypothesis (see also SCHOLANDER *et al.*, 1953) that the temperature-growth rate relationship in aquatic insects is as much a reflection of the environments in which a species' ancestors lived as it is of the environment in which the species now lives. In other words, evolution has been conservative, and temperate-zone species that belong to families that have mainly tropical distributions (e.g. Odonata) are expected to have temperature-growth rate relationships more similar to those of their tropical relatives than to sympatric species that belong to predominantly temperate-zone families.

In order to explore this hypothesis we have taken certain parameters of the temperature-development relationship and compared them between

species. We have used the power equation to describe the relationship mathematically :

$$\ln D = \ln a + b \ln T$$

where D is the number of heat units (time multiplied by degrees above 0°C) required to complete a portion of development at temperature T, and we use the constants a and b for comparative purposes. a is the number of heat units required to complete development at 1°C and b is the slope of the regression of D on T.

The number of heat units involved in completion of a particular phase of an insect's development is a measure of the thermal energy necessary to drive the metabolic processes involved. When the slope of the heat units – temperature curve is not zero (the majority of examples available), different amounts of thermal energy are required at different temperatures. The lowest point on this curve thus represents *one* measure of optimal temperature for growth, and curves that have lower absolute slope values (the slope of the line is usually negative but can be positive) may be interpreted as showing adaptation to a wider range of temperatures.

The intercept, a, is also a measure of temperature adaptation since it implies that, if the power equation is a reasonable descriptor, if species are similar in size, and if the species could develop at 1°C, those species with high values for a would take longer to develop at this temperature than would those with low values.

We have found that temperate-zone aquatic insects, like the Plecoptera, which probably experience a wide temperature range, have low slopes and low intercept values (*Taeniopteryx nebulosa* in Fig. 1). Tropical, warm-water species, like the mosquito *Toxorhynchites brevipalpis* (Fig. 1), which probably experience little temperature variation, have high negative slopes and high intercept values.

In this paper we have collected together all available data on the relationship between rate of development of Odonata eggs and temperature, and we compare these one species with another and with data from other aquatic insects. We restrict ourselves to the egg stage because rates of development of eggs can be related to temperature alone ; the confounding effects of feeding regime which affects larval comparisons is absent, as is diapause in general. PRITCHARD & MUTCH (1985) have treated mosquitoes in this way and this paper should be consulted for a fuller account of the methods and a review of the problems encountered in extraction of data from the literature.

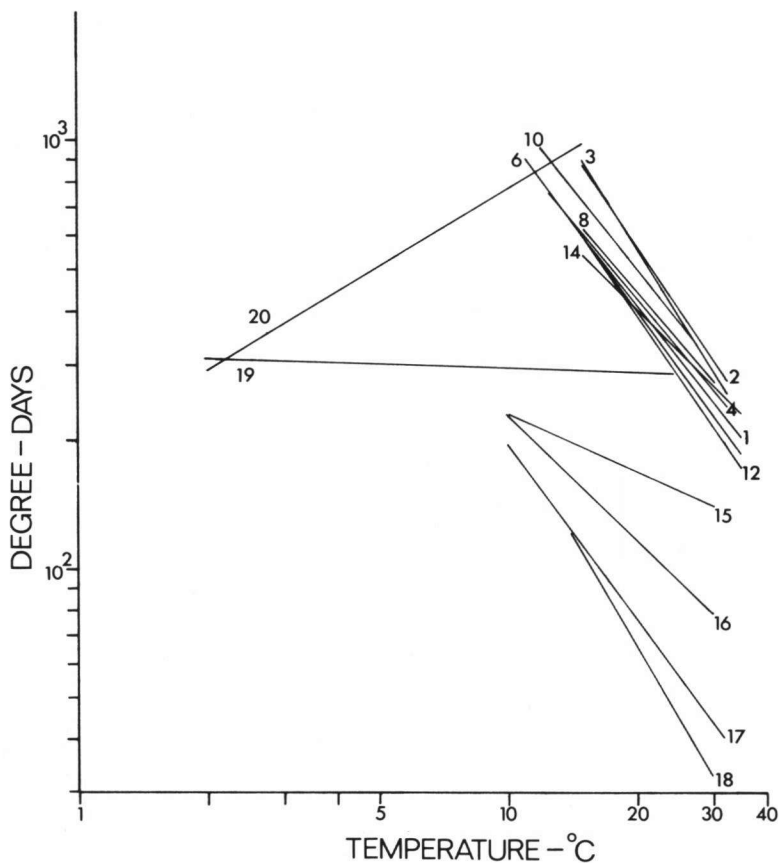


Fig. 1. Power curves relating temperature to the number of degree-days required to complete embryonic development in some mosquitoes, stoneflies and dragonflies. Numbers refer to the species listed in Tables I and II.

## RESULTS

Only 14 data sets are complete enough for analysis. Of these, 11 are from Canada at latitudes between  $46^{\circ}$  and  $51^{\circ}$ N, 2 are from the United States at latitudes of  $39^{\circ}$  and  $42^{\circ}$ N, and 1 is from Europe at  $48^{\circ}$ N. The power equations are presented in Table I. In Table II are given the power equations for 4 species of temperate-zone mosquitoes (PRITCHARD & MUTCH, 1985), 2 species of stoneflies (BRITTAIN, 1977 ; BRITTAIN & MUTCH, 1984), and *Enallagma boreale* from Alberta (present study). The power curves for all of

these species except for *Enallagma boreale* from Quebec and *Platthemis lydia* are shown in Fig. 1.

The 3 taxonomic groups (Odonata, Plecoptera, Culicidae) form 3 distinct families of curves. The Plecoptera have very low or positive slope values and low intercept values ( $2-3 \times 10^2$ ). The mosquitoes have a range of negative slope values from intermediate to very high, and intermediate intercept values ( $6-116 \times 10^2$ ). The Odonata form a distinct group with high to very high slope values and high intercept values ( $6-430 \times 10^3$  with most values  $15-35 \times 10^3$ ).

Table I

Parameters of the power equation relating day-degrees to temperature in eggs of Odonata.  
ab = Alberta, bc = British Columbia, id = Idaho, ost = Austria, que = Quebec, va = Virginia

Species	Location	a	b	r <sup>2</sup>	Reference
<i>Ischnura verticalis</i>	que	17656	- 1.26	0.99	FRANCHINI & PILON 1983
<i>Enallagma vernale</i>	que	47565	- 1.48	1.00	PILON 1982
<i>Enallagma ebrium</i>	que	68362	- 1.61	0.98	PILON 1982
<i>Enallagma hageni</i>	que	15519	- 1.20	0.99	MASSEAU & PILON 1982
<i>Enallagma boreale</i>	que	2786111	- 2.78	0.98	RIVARD <i>et al.</i> 1975
<i>Enallagma boreale</i>	ab	24473	- 1.38	0.99	PRITCHARD & LEGGOTT unpub
<i>Argia vivida</i>	bc	31596	- 1.40	0.99	LEGGOTT & PRITCHARD 1985
<i>Argia vivida</i>	ab	14574	- 1.17	1.00	LEGGOTT & PRITCHARD 1985
<i>Argia vivida</i>	id	6442	- 0.93	1.00	LEGGOTT & PRITCHARD 1985
<i>Coenagrion puella</i>	ost	21754	- 1.26	1.00	WARINGER & HUMPESECH 1984
<i>Platthemis lydia</i>	va	430925	- 2.38	0.99	HALVERSON 1983
<i>Leucorrhinia borealis</i>	ab	30303	- 1.46	1.00	LEGGOTT & PRITCHARD unpub
<i>Leucorrhinia proxima</i>	ab	32761	- 1.48	1.00	LEGGOTT & PRITCHARD unpub
<i>Cordulia shurtleffi</i>	ab	8134	- 1.01	0.99	LEGGOTT & PRITCHARD unpub

Table II

Parameters of the power equation relating degree-days to temperature in Culicidae,  
Plecoptera and Odonata.

ab = Alberta, al = Alabama, il = Illinois, no = Norway, Su = Sudan

Species	Location	a	b	r <sup>2</sup>	Reference
<i>Aedes sticticus</i>	ab	646	- 0.45	0.98	TRPIS <i>et al.</i> 1973
<i>Aedes vexans</i>	il	2062	- 0.96	0.98	HORSFALL <i>et al.</i> 1973
<i>Anopheles quadrimaculatus</i>	al	4574	- 1.37	0.98	HUFFAKER 1944
<i>Toxorhynchites brevipalpis</i>	su	11606	- 1.73	0.99	TRPIS 1972
<i>Taeniopteryx nebulosa</i>	no	313	- 0.03	0.99	BRITAIN 1977
<i>Mesocapnia oenone</i>	ab	197	+ 0.41	0.99	BRITAIN & MUTCH 1984
<i>Enallagma boreale</i>	ab	24473	- 1.38	0.99	PRITCHARD & LEGGOTT unpub

## DISCUSSION

The family of equations for Odonata forms a distinct group that clearly fits into the "warm-adapted" category. Intercept values are very high, indicating a very large heat energy requirement for development at low temperatures. Slope values are high and negative indicating adaptation to a narrow range of high temperature. Optimum temperature, defined by minimum heat energy requirement, is 30-35°C. By contrast, mosquitoes from the same latitude (*Ae. sticticus* and *Ae. vexans* in Fig. 1 ; see also PRITCHARD & MUTCH, 1985) have lower slope values, and the stoneflies are clearly "cold-adapted".

Unfortunately there are insufficient data available to examine whether adaptation to prevailing temperature regimes has occurred in Odonata eggs, as it appears to have done in mosquitoes (PRITCHARD & MUTCH, 1985). There are currently no data available for Odonata from tropical habitats, and in a comparison between 3 populations of *Argia vivida* inhabiting sites with different thermal regimes, neither the slope values nor the intercepts were significantly different, although there were trends appropriate to the hypothesis that adaptation had occurred (LEGGOTT & PRITCHARD, 1985). The most southerly dragonfly considered here (*Plathemis lydia*) does indeed have very high slope and intercept values. However, the data used to generate the power equation were obtained from HALVERSON'S (1983) hyperbolic equation and were not the actual raw data ; thus these values must be considered suspect. The very high values obtained for *Enallagma boreale* from Quebec are also suspect, because they are so different from those for *E. boreale* from Alberta and from the other *Enallagma* from Quebec.

A reason, why we might not expect to find differences amongst the dragonflies and between the dragonflies and tropical mosquitoes, but would expect to find differences between the dragonflies and both the stoneflies and the temperate-zone mosquitoes, becomes apparent when the ambient temperature in nature at the time of oviposition is considered. The stoneflies oviposit into very cold water (*Mesocapnia oenone* eggs actually develop over winter) and the egg is the overwintering stage of north temperate-zone *Aedes* mosquitoes. By contrast all of the dragonflies here considered oviposit into relatively warm water. Thus there is no reason to believe that adaptation should have occurred in the egg stage of most temperate-zone dragonflies. However, larvae might be expected to differ between tropical and temperate sites.

## ACKNOWLEDGEMENT

Financial support from the Natural Sciences and Engineering Research Council of Canada to the senior author is gratefully acknowledged.

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