



Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments

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Average reaction norms relating number of day-degrees required to complete egg development to temperature are described for 95 species (115 populations) of Plecoptera, Odonata, Ephemeroptera, and Diptera (mainly Culicidae, with some Tipulidae and Sciomyzidae). The slope of the average reaction norm is used as an index of adaptation, with positive slopes indicating cold-adapted species, negative slopes indicating warm-adapted species, and slopes around zero indicating generalist species; 57% of the between-taxon variation in slope is associated with differences between orders, 14% among families, 7% among genera, 14% among species, and 8% among populations. Significant differences between congeneric species are found in only 4 of 92 possible comparisons. Only Plecoptera show much cold-adaptation, with 40% of the species having significantly positive slope. However, 26% of the species (mainly in the Systelognatha) have significantly negative slope, suggesting adaptation to warmer waters than those in which the order is believed to have originated. The other orders probably originated in warm water and have generally maintained this adaptation. All Odonata, 71% of the Diptera and 81% of the Ephemeroptera have significantly negative slopes. Diapause is a common alternative to metabolic adaptation to deal with unfavourable thermal environments. We suggest that it occurs widely in eggs of Plecoptera and in the mayfly *Rhithrogena loyolaea*, cold-adapted species that may use diapause to survive periods of high temperature.

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ADDITIONAL KEY WORDS:—Thermal reaction norms – metabolic adaptation – diapause – Ephemeroptera – Odonata – Plecoptera – Diptera.

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INTRODUCTION

Life-history evolution facilitates invasion of new environments by reweighting the relative importance of individual components, such as age at first reproduction, fecundity and longevity. However, because life-history components are not in themselves unitary characters (Cole, 1954; Stearns, 1976, 1992), even minor life-history shifts can involve many aspects of an organism's biology. For example, age at first reproduction integrates all of the developmental processes leading to reproductive maturity and their survival consequences, so that evolution of earlier reproduction could have wide-ranging consequences. Given the complexity of life-history components, tradeoffs between their constituent traits (Istock, 1967; Sibly & Calow, 1986; Stearns, 1989a) are common. These tradeoffs help govern the course of life-history evolution by simultaneously limiting the diversity of adaptive character combinations and delineating alternative strategies with equivalent fitness (Partridge & Sibly, 1991).

Many life-history traits of ectotherms exhibit marked phenotypic plasticity because of the dependence of metabolism and development on temperature. As a result, life-history evolution for ectotherms could directly alter the optimal set of phenotypes expressed by a genotype in different thermal environments (norm of reaction: Schmalhausen, 1949; Stearns, 1989b; Via *et al.*, 1995). Alternatively, the plasticity of thermal responses may retard such evolution and encourage the evolution of qualitatively different responses to dissimilar thermal environments. Via & Lande (1985) showed theoretically that genetic correlations among the states of a character in different environments can substantially impede evolution of reaction norms. Such retardation of evolution could shift the balance in favour of an alternative, less plastic, strategy.

There is a body of data that suggests that modification of thermal reaction norms is not a common strategy in insects. In contrast to their results for fish and crustaceans, Scholander *et al.* (1953) found that related arctic and tropical species of terrestrial insects exhibited very similar metabolic responses to different temperatures. Similarly, Lee & Baust (1982) concluded that the Antarctic chironomid fly, *Belgica antarctica* did not show metabolic cold adaptation. Similar conservatism was shown in a comparison of egg development in temperate and tropical aquatic insects (Jackson & Sweeney, 1995). Downes & Kavanaugh (1988: 3) even proposed, "not only that a species is generally characteristic of a particular life zone or other area with a somewhat restricted range of climatic variation, but also that the genus or other higher taxon to which it belongs is similarly, if perhaps more broadly, restricted." On the other hand, studies that do suggest metabolic evolution in terrestrial arthropods from high latitudes have been criticized on methodological grounds (Cossins & Bowler, 1987: 194). MacLean (1975) pointed out that there are several ways, besides metabolic adaptation, in which invertebrates cope with arctic tundra environments, and Cossins & Bowler (1987: 195) concluded that "it is clear that Antarctic species are not simply temperate species shifted with metabolic

compensation to a lower range of temperatures, but have evolved a particular suite of adaptive characteristics which uniquely match them to their peculiar habitats." Within this suite of adaptive characteristics, metabolic cold-adaptation is probably unimportant in polar marine invertebrates (Clarke, 1980). This is not to say that all aspects of insects' responses to temperature are restricted. Minimum lethal temperatures are often higher for tropical insects than for temperate species (Chapman, 1982), and temperature optima for larval development in coenagrionid dragonflies are higher in warm spring species than in species that inhabit cold water (Pritchard, unpublished data).

An alternative strategy to shifts in enzyme systems that determine the thermal reaction norm, is the evolution of diapause. Diapause "routes the metabolic programme of the organism away from direct developmental pathways and into a ... clearly organized break in development" (Danks, 1987: 9–10). This organized break in direct or normal development has been called "diapause development" (e.g. Tauber, Tauber & Masaki, 1986: 52–53). Although the control of diapause development is complex and not well understood, it is an active process (Danks, 1987: 133 ff.), and thermal reaction curves for the completion of diapause are quite different from those for direct development (Lees, 1955; Danks, 1987: 149–150). The range of temperatures within which diapause is completed is usually shifted downward and, in some species at least, low temperatures apparently hasten the completion of diapause and high temperatures maintain insects in diapause (Tauber *et al.*, 1986; Marten & Zwick, 1989; Økland, 1991).

In this paper, we examine the impact of temperature on development time for eggs of 95 species of aquatic insects. Use of eggs, rather than active stages of the life-cycle, avoids some of the problems that can afflict interspecific comparisons (Cossins & Bowler, 1987), and development rates do not vary with external feeding regimes. Our analysis of thermal adaptation examines two main questions. First, do related species exhibit different average reaction norms as expected from the evolution of thermal adaptations to different environments? Such differences in reaction norms have been observed previously for the eggs of other aquatic poikilotherms (e.g. frogs: Moore, 1939, 1949; copepods: McLaren, Corkett & Zillioux, 1969). Second, is taxonomic relatedness correlated with limited observed variation in average reaction norms, as Downes & Kavanaugh (1988) proposed? Furthermore, we examine the possible implication of diapause as an explanation for our results.

THEORETICAL BACKGROUND AND EXPECTATIONS

Within the viable temperature range, the time (D) required for an insect that is not in diapause to complete part of its development, such as the egg stage, generally decreases with increasing temperature (T) according to a reaction norm that can be adequately represented by a power function:

$$D = pT^q \quad \text{eqn 1}$$

where p is the average development time at 1°C and q determines the rate of change in development time with changes in temperature ($q < 0$ for insect development). Therefore, evolutionary modification of thermal responses will necessarily involve a shift in the average reaction norm for a population.

Instead of simple time (days), our analysis of thermal adaptation will consider physiological time, a biologically more relevant measure embodied in the thermal sum, S (day-degrees):

$$S = \int_0^D (T_t - \tau) dt$$

where T_t is the temperature at time t and τ is some fixed temperature above which thermal energy is measured (for this study $\tau = 0^\circ\text{C}$). When development time (D) is measured at a fixed temperature (T), as in this study, the thermal sum simply becomes DT .

Now consider the power function relating development to temperature (eqn. 1), with development time replaced by the thermal sum:

$$DT = aT^b \quad \text{eqn 2}$$

We use linear regression to analyse the logarithmic transformation of this relation,

$$\ln(DT) = \ln a + b \ln(T) \quad \text{eqn 3}$$

Such an analysis results in mathematically identical results to the corresponding analysis of eqn 1, except that $b = q + 1$ and the corresponding coefficient of determination (r^2) generally decreases: all other statistics, including a , remain unchanged (Appendix 1). Based on such a regression analysis, b estimates the slope of the population average reaction norm for egg development.

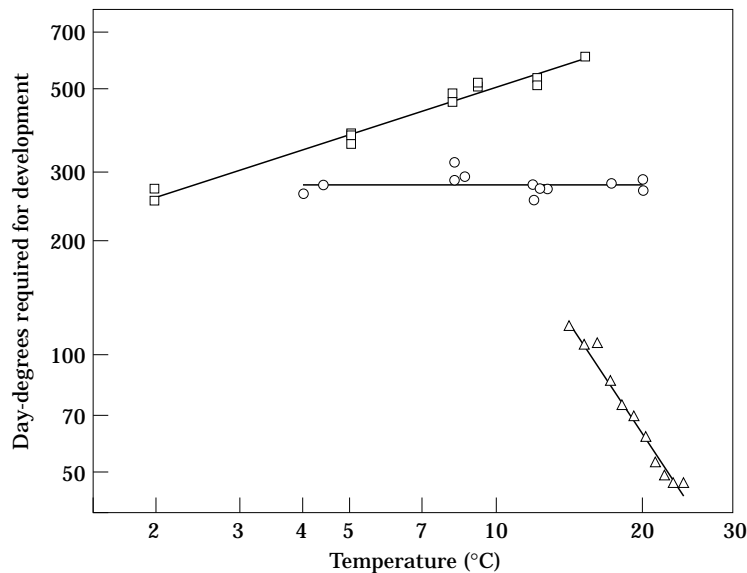


Figure 1. Examples of three categories of thermal reaction norms for egg development: (□) fewer day-degrees above 0°C required at low temperatures indicates adaptation to low temperature (*Mesocapnia oenone*, Plecoptera. Data from Brittain & Mutch, 1984); (△) fewer day-degrees above 0°C required at high temperatures indicates adaptation to high temperatures (*Toxorhynchites brevipalpis*, Diptera. Data from Trpis, 1972); (○) a slope value near zero indicates adaptation to a variable temperature regime (*Taeniopteryx nebulosa*, Plecoptera. Data from Brittain, 1977).

If there is an advantage to rapid egg development (reduction of predation risk, avoidance of unpredictable disturbances, increase in potential rate of increase), the slope of the thermal reaction norm (b) should generally reflect the thermal adaptation for a given species. Pritchard & Mutch (1985) and Pritchard & Leggott (1987) defined warm- and cold-adapted species on this basis, and Mutch & Pritchard (1986) extended the analysis to include three categories of thermal adaptation. Cold-adapted insects are those exhibiting positive slopes when thermal sum for development is plotted against temperature (Fig. 1, squares), because development requires less thermal energy at lower temperatures. Aquatic insects with such characteristics should be found in arctic and alpine waters and cold springs. In contrast, warm-adapted insects, such as those found in tropical lowland habitats and warm springs, should have negative slopes (Fig. 1, triangles). Finally, insects that occupy habitats with variable temperature regimes, such as temperate-zone lakes, ponds and rivers, should exhibit shallow or zero slopes (Fig. 1, circles), showing equally efficient growth at all temperatures in the favourable range. This pattern was used by Lillehammer *et al.* (1989), but Brittain (1990) used both the slope and the intercept of the thermal reaction norm to compare egg development in mayflies and stoneflies, as Pritchard & Mutch (1986) had done for mosquitoes. He introduced the terms "thermal demand" (the intercept, $\ln a$; see eqn 3) and "temperate dependency" (the slope, b). Marten (1990) correctly pointed out that the intercept is a measure of thermal demand only at 1°C (see also Pritchard & Mutch, 1985). Furthermore, $\ln(a)$ and b are usually inversely related because, if two reaction norms intersect at some temperature above 1°C, a steeper slope for one reaction norm will be associated with a lower intercept (White & Gould, 1965). Thus, we use the slope alone as a composite measure of temperature adaptation. Also, the intercept is correlated with egg size (Lillehammer *et al.*, 1989), whereas slope is not. Marten (1990) seems to have misunderstood Mutch & Pritchard's (1986) classification and he developed a new measure ("integrated development time" or IDT) to compare thermal requirements of different species. IDT integrates the area under the temperature/development time curve, and so is dependent on the value of a . Thus, it may not distinguish between warm-adapted species that have high thermal demand at low temperatures and cold-adapted species that have a high thermal demand at high temperatures. Therefore, we still prefer Mutch & Pritchard's (1986) classification, which is based solely on the slope of the thermal reaction norm.

Diapause complicates interpretation of thermal reaction norms because an insect in diapause does not respond to temperature as it does when undergoing normal development. Mutch & Pritchard (1986) noted that diapause can result in development that appears to be temperature independent (i.e. $b \approx 1$). If the thermal reaction norm for completion of diapause is the exact reverse of that for normal development (insects complete diapause more rapidly at *lower* temperatures), complete development involving a phase of normal development and a phase of diapause could appear to be temperature-independent as shown in Figure 2B. In fact, variation in the intensity of diapause (measured by the time to complete diapause at a given temperature: the more intense the longer the time) could produce a complete range of relationships between temperature and time to complete development, from a normal negative relationship (Fig. 2A) when diapause is not particularly intense, to a positive relationship when diapause is intense (Fig. 2C). Furthermore, if there is a relationship between intensity of diapause and increasingly positive b , species with steep positive slopes should have lower thermal maxima in

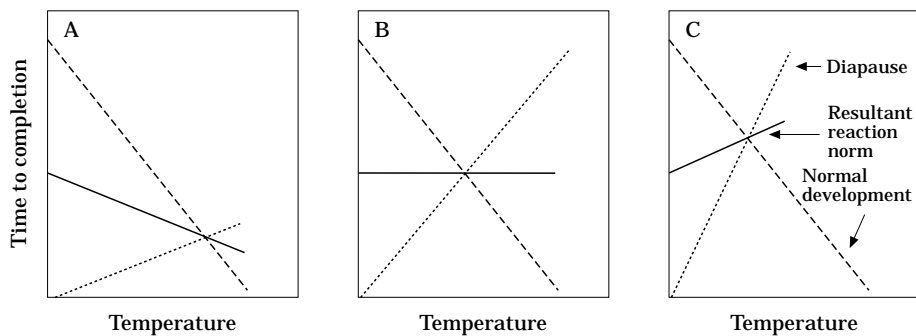


Figure 2. Hypothetical relationships between temperature and time to complete normal development (---), diapause (...) and the observed (composite) reaction norm (—), given increasing intensities of diapause (A, B, C). As the intensity of diapause increases, indicated by longer diapause at a given temperature, the slope of the observed reaction norm becomes increasingly positive. Panel B indicates apparent temperature independence of time to complete development.

constant temperature experiments than species with negative slopes, because intense diapause requires a very long time for completion at higher temperatures.

METHODS

We analysed the data on the development of aquatic insect eggs at fixed temperatures extracted from 112 published studies and four unpublished studies. This survey included 46 species (54 populations) of Plecoptera, 14 species (16 populations) of Odonata, 21 species (29 populations) of Ephemeroptera, and 14 species (16 populations) of aquatic Diptera (Appendix 2). Most of these data were collected by recording at intervals of no more than one day the number of eggs that hatched at several fixed temperatures. In our own work, we use median development time, obtained from observations at 4 h intervals during the hatching period. Some studies report time to first hatch (minimum development time), rather than mean or median development time. Such data are obviously subject to considerable error; we note these studies in Appendix 2, and they should be interpreted accordingly. Data were accepted in various forms. We preferred medians or means at each temperature, but have also extracted data from histograms or graphs, or used published power equations if these were the only data presented and if the work satisfied the criteria outlined below.

Sometimes we had to decide whether to include all of the data from a particular study. The power curve describes the relationship between development time and temperature within a thermal range that is favourable for development. It is important that data from the full favourable range of temperatures be included when assessing eqn 3, because omission of points from either end can markedly affect parameter estimates. Development is often measured inadequately at lower temperatures because of technical problems that develop over the very long periods necessary in work at temperatures close to the thermal minimum (disease, equipment failure). Thus, we did not use data from studies in which temperature selection was clearly biased towards higher temperatures. It is also important that temperatures above the thermal maximum not be included when fitting eqn 3. We define the

thermal maximum as that temperature above which the number of day-degrees (species with negative or zero slope thermal reaction norms) or days (species with positive reaction norms) required to complete development begins a consistent increase. We frequently reanalysed other authors' data to exclude observations above the thermal maximum. Fortunately, most experiments include temperatures above the thermal maximum and so this end of the favourable range can usually be established.

Many dipteran eggs require a particular sequence of environmental factors, such as drying and wetting, to elicit hatch, even though embryogenesis may be complete. These latent periods can be experimentally separated from the period of active development, but generally they introduce difficulties into the collection of data on temperature responses. For these same reasons, we did not try to separate phases of diapause from phases of normal development in data on eggs with diapause. In general, we did not use studies in which diapause was clearly recognized, because a different set of experimental temperatures was generally used to break diapause than was used during the phases of normal development. However, data from eggs with a period of diapause development which was completed at the experimental temperatures without any manipulation, proved invaluable in incorporating the effect of diapause on thermal reaction norms in our analysis.

Other authors (e.g. Campbell *et al.*, 1974; Nealis, Jones & Wellington, 1984), working with terrestrial insects, have used developmental zero, rather than b , to show temperature adaptation. A linear regression of slope (b , eqn 3) on developmental zero (the intercept of the linear regression of development *rate* on temperature) for 40 species of Plecoptera, Odonata, and Diptera had an r^2 of 0.94, showing that both parameters relate similar information (Fig. 3). We prefer slope as a measure of temperature adaptation for two reasons. First, it can be estimated when

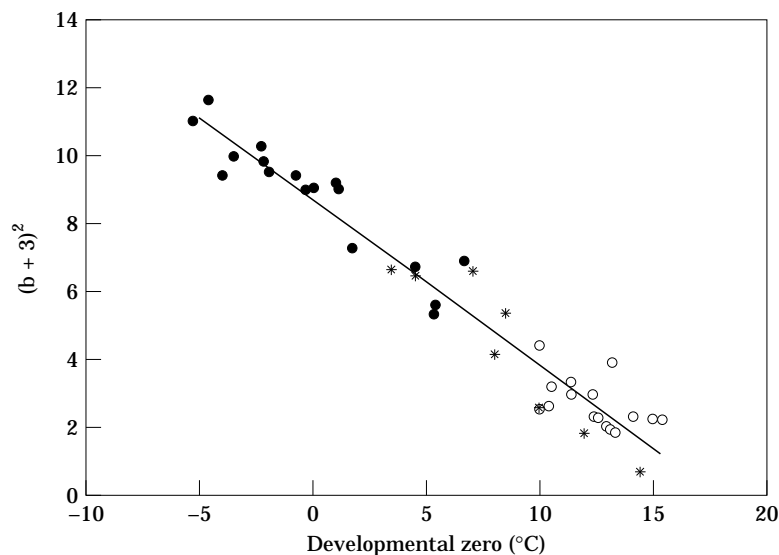


Figure 3. The relationship between average slope of thermal reaction norm (b) and estimated developmental zero for 40 populations of Odonata (open circles), Plecoptera (closed circles), and Diptera (stars). The value of 3 is added to b to remove negative values before squaring.

developmental zero cannot (e.g. very cold-adapted species with rates of development independent of temperature). Second, developmental zero is usually estimated as the X -intercept from a linear regression of rate of development against temperature. However, the relationship between rate of development and temperature is rarely linear and the straight line can be fitted only to the middle portion of the curve (which approaches linearity), in which case the developmental threshold is overestimated (and development may be observed at temperatures below the estimated developmental zero). Alternatively, all of the data may be included in the regression, in which case the value for the thermal threshold depends on the range of available data points.

RESULTS

A nested analysis of variance revealed that over half (56.6%) of the between-taxon variation in slope was associated with differences between orders ($F_{3,11} = 8.76$, $P < 0.005$). The remaining variance was distributed among families (13.69%; $F_{16,14} = 2.32$, $P > 0.05$), genera (7.33%; $F_{17,46} = 1.77$, $P > 0.05$), species (14.41%; $F_{43,19} = 3.24$, $P < 0.005$), and populations (7.97%), in much smaller proportions. The significant differences between species within genera resulted from only four of 92 possible comparisons: *Aedes aegypti* differed significantly from *A. sticticus*; *Rhithrogena loyolaea* differed from *R. semicolorata*, and *Isoperla obscura* differed from both *I. grammatica* and *I. difformis* (based on Tukey's multiple comparisons, $P < 0.05$ in all cases). The two *Aedes* species are at opposite ends of a latitudinal range and thermal adaptation may have occurred in *A. sticticus* (Pritchard & Mutch, 1985). *Isoperla obscura* has an egg diapause (Økland, 1991), as probably does *Rhithrogena loyolaea* (see below).

Variances were compared with Hartley's F_{\max} test (Sokal & Rohlf, 1981) with Bonferroni-adjustment of the Type I error rate to accommodate multiple contrasts (Neter, Wasserman & Kutner, 1990). The Odonata was the least variable order and the variance of slope-values (b) for dragonflies ($s^2 = 0.049$, $n = 16$) was significantly smaller than the variances for all other orders ($P < 0.05$). The Plecoptera were next least variable ($s^2 = 0.137$, $n = 43$), although their slope-value variance did not differ significantly from that of the Ephemeroptera ($s^2 = 0.323$, $n = 24$). Dipterans exhibited the greatest variation between species in the slopes of average reaction norms ($s^2 = 0.491$, $n = 16$), although they too did not differ significantly from the Ephemeroptera.

All of the species of Odonata have significantly negative slopes (Fig. 4), as do most Ephemeroptera (81%) and Diptera (71%), but only 26% of the Plecoptera (this value includes *Nemoura pictetti*, *N. cinerea*, *Leuctra hippopus*, and *Diura bicaudata*, one population of which has a significantly negative slope, but a second population of each has a non-significant or significantly positive slope). Except for one ephemeropteran (*Rhithrogena loyolaea*) and one dipteran (*Ilione albiseta*), only the plecopterans have significantly positive slopes. In the Plecoptera, 40% have positive slopes (including *Utacapnia trava*, *Leuctra hippopus*, and *Diura bicaudata*, one population of which has a significantly positive slope, but another population has a non-significant slope or a significantly negative slope). The plecopterans also have the lowest thermal maxima, overlapping with the Ephemeroptera but separate from the Culicidae and Odonata (Fig. 5). They also differ from the other groups (if *R. loyolaea* is excluded) in showing

a significant regression of slope on thermal maximum (Fig. 5), a result that may mean that plecopteran eggs typically enter diapause (see Theoretical Background & Expectations).

DISCUSSION

Temperature-development characteristics of different taxa

The commonness of positive slopes of average reaction norms only among the stoneflies (Fig. 4), shows that, among the orders considered, only Plecoptera show frequent cold-adaptation. This appears to be the primitive condition in this order, as it probably originated in the southern-hemisphere temperate zone and crossed tropical regions during the Permian Ice Age (Illies, 1965). Most of the present-day

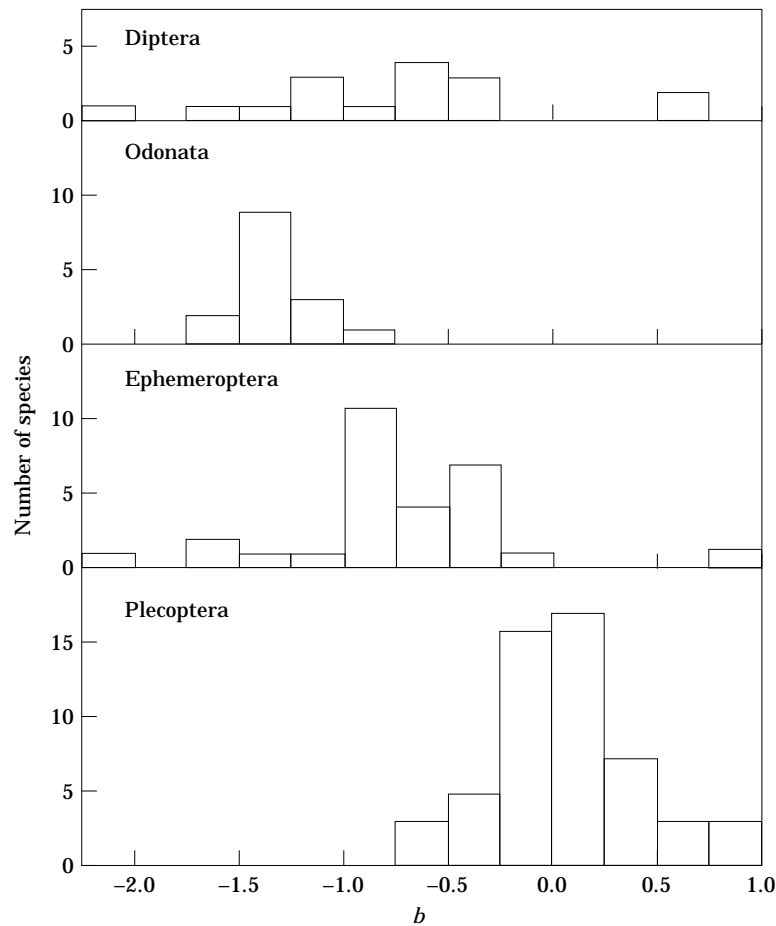


Figure 4. Frequency distributions of slopes of average thermal reaction norms (b) for egg development for four orders of aquatic insects. Positive slopes indicate cold adaptation because fewer day degrees are required to complete development at lower temperatures. Increasingly negative slopes indicate warm adaptation.

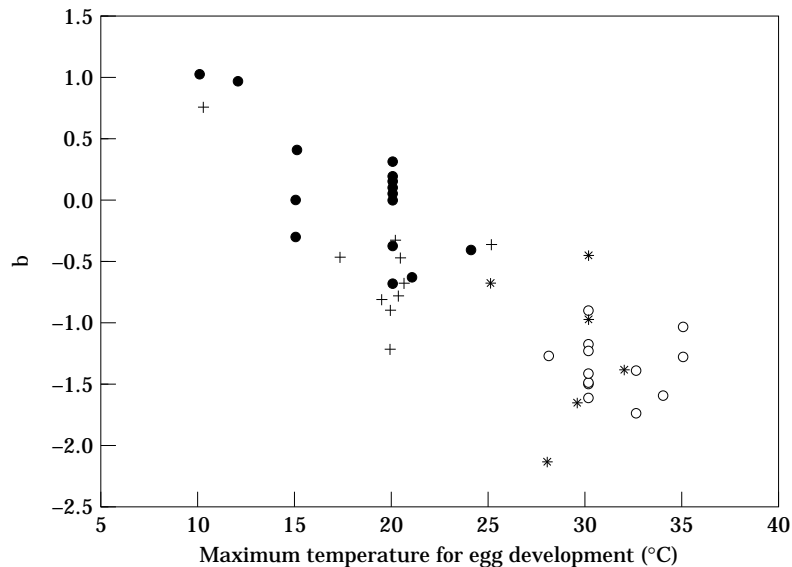


Figure 5. The relationship between average slope of thermal reaction norms (b) and maximum temperature for egg development for 16 populations of Odonata (open circles, $b = 0.0057$, $t = 0.2$, $df = 14$, $P = 0.8440$), 18 Plecoptera (closed circles, $b = -0.0897$, $t = -3.87$, $df = 16$, $P = 0.0014$), 7 Culicidae (stars, $b = -0.0011$, $t = -0.01$, $df = 5$, $P = 0.9937$), and 11 Ephemeroptera (crosses, $b = -0.0960$, $t = -2.63$, $df = 9$, $P = 0.0273$; without *R. loyolaea* (highest ephemeropteran value) $b = 0.0412$, $t = 0.81$, $df = 8$, $P = 0.4433$).

tropical species of Plecoptera belong to the 'family-group' Systellognatha within the suborder Arctoperlaria (see Zwick, 1980 for plecopteran phylogeny). Although all of our Plecoptera data are from temperate species, warm-adapted eggs ($P < 0.05$) are found in seven of the thirteen systellognathan species. The perlid, *Perla burmeisteriana* also has a steep negative slope (Marten, 1991) that would certainly be significant were the raw data available for the determination of error. Two other systellognathans (*Isoperla grammatica* and *Isogenus nubecula*) have non-significant slopes, and four (*Chloroperla tripunctata*, *Perlodes microcephala*, *Isoperla obscura*, and a stream population of *Diura bicaudata*) have positive slopes. Of these, at least the last two have an egg diapause (Økland, 1991; Elliott, 1995). By contrast, only five of 34 species in the Euholognatha (the sister taxon of Systellognatha) show this level of warm adaptation. It is interesting that the Southern Hemisphere Notonemouridae and the Northern Hemisphere Nemouridae, which are considered sister taxa within the Euholognatha (Zwick, 1980), have similar ranges of reaction norms, with most slopes not differing significantly from zero (Brittain, 1991). Thus, some Plecoptera have apparently adapted to new thermal environments, but the stoneflies have generally remained in the cool waters in which they probably evolved. Unfortunately, although Hynes & Hynes (1975) present some data on egg development in the suborder Antarctoperlaria, the least derived taxon of Plecoptera (Zwick, 1980), these are insufficient to calculate thermal relationships.

The Odonata are quite different from the Plecoptera. Dragonflies only occupy water that is warm for at least part of the year and generally survive periods of low temperature as cold-resistant larvae. Temperate-zone Odonata have universally adopted diapause (generally as larvae) as a means of synchronizing cold-sensitive

stages with warm conditions (Corbet, 1980; Norling, 1984). Like stoneflies, all dragonfly data sets are from temperate latitudes; however, unlike the stoneflies, the slopes for dragonfly eggs form a close, warm-adapted group. The high intercepts for odonates (Appendix 2) show a very large heat-energy requirement for development at low temperatures, and the steep, negative slopes (Fig. 4) show adaptation to high temperatures. Optimum development temperature, defined by the minimum heat energy requirement for embryogenesis and hatching, is 30–35°C (Fig. 5). As expected from these results, all of the dragonflies considered oviposit into relatively warm water during summer. The Odonata originated in tropical environments (Pritchard, 1982). Although many larvae, some eggs, and a few adults can survive cool temperatures, no egg development occurs below about 10°C and optimal temperatures for growth and activity of all stages are above 20°C (Pritchard, 1982; Pritchard & Leggott, 1987). Thus dragonflies have apparently retained the temperature characteristics of their ancestors, even when they occupy very different environments from those of their ancestors.

The evolutionary history of the Ephemeroptera is unclear. Mayflies are common in the tropics, but possibly not as diverse as in the temperate zone (Wolda & Flowers, 1985). Twenty-two of the North and Central American genera are believed to have had a tropical origin, whereas 39 are boreal (Edmunds, Jensen & Berner, 1976). In addition, many mayflies live in cold environments and undergo quiescence or diapause as eggs or larvae during summer (Newbold, Sweeney & Vannote, 1994). If the Ephemeroptera and Odonata are sister-groups (Kukalova-Peck, 1985), they might have shared a tropical origin. Indeed, the eggs of almost all of the temperate-zone mayflies included in this review are warm-adapted (Fig. 4), although generally less so than the Odonata. The sole tropical species included here (*Euthyplocia hecuba*) is quite warm-adapted. The single cold-adapted species of Ephemeroptera (*Rhithrogena loyolaea*) rarely hatches above 10°C and is restricted to cold European mountain streams (Humpesch & Elliott, 1980). It possibly has an egg diapause, and this would explain the significant difference in slope of reaction norm between this species and *R. semicolorata*.

Like the odonates, mosquitoes were originally tropical and many species that have successfully colonized temperate zones include diapause in their life-histories as a means of surviving low temperatures (Clements, 1963). Not surprisingly, all culicids for which data are available have negative slopes like the odonates (Fig. 4). However, unlike dragonflies, mosquitoes apparently have adapted to the lower temperatures of higher latitudes, because there is a distinct trend for shallower slopes in species that range farther north (Pritchard & Mutch, 1985). Hence the slopes of reaction norms for *Aedes aegypti* and *A. sticticus*, which are at opposite ends of the latitudinal range, differ significantly.

The Tipulidae may also have had a tropical origin (Pritchard, 1983), although Tipulinae are not as well represented in the Neotropics today as are Limoniinae (Byers, 1982). The two temperate-zone species of *Tipula* for which we have adequate data have negative slopes, which are similar to those of mosquitoes from similar latitudes. On the other hand, among the Sciomyzidae, the Sciomyzinae at least are considered a cool-adapted group (Berg & Knutson, 1978), but Gormally's (1985) data are too variable to confirm this; one species has a significant positive slope, but the other two (one positive, one negative) are not significant. It is unfortunate that data are not available for the Chironomidae, because most subfamilies are believed

to be cold-adapted (Oliver, 1981), although some species live in geothermal springs (Pritchard, 1991).

Effect of diapause

Although we excluded some species that were known to have an egg diapause, the intensity of diapause varies and so it is not always easy to detect. Given our expectation that diapause should be (a) more intense in species with positive slopes and (b) inversely correlated with the maximum temperature at which development occurs, diapause should occur widely in Plecoptera and in at least one species of Ephemeroptera (Fig. 5). In contrast, none of the other species of Ephemeroptera nor any of the Odonata or Culicidae that we have considered should have an egg diapause. In the Plecoptera, the order with the most positive slopes, diapause occurs in both eggs and larvae (e.g. Khoo, 1968; Harper & Hynes, 1972; Marten & Zwick, 1989; Økland, 1991; Elliott, 1995) and usually serves in avoiding warm conditions. In our review, the species with the steepest positive slopes are the mayfly *Rhithrogena loyolaea*, and the stoneflies *Amphinemura banksi*, *Isoperla obscura*, and the stream population of *Diura bicaudata*. These species oviposit in perpetually cold water, implying that they cannot tolerate warm conditions. An egg diapause would prolong development considerably should conditions warm, allowing survival until cold conditions return. For example, eggs of *R. loyolaea*, placed in an unnatural habitat, developed but did not hatch in 4 months, presumably because conditions were too warm for the completion of diapause (Humpesch & Elliott, 1980), and Økland (1991) has shown that eggs of *Isoperla obscura* require temperatures below 12°C for the completion of diapause development.

However, a graded diapause response does not explain why species with negative slopes do not develop at low temperatures (< 5°C), unlike species with positive slopes. Although diapause is completed more rapidly at low temperatures, species with diapause must still complete normal development. Why should they be better able to do this at low temperatures than species without diapause? Presumably because their enzyme capability has become specialized to function at low temperature. However, because enzymes have limited ranges of active temperatures (Hochachka & Somero, 1984), any poikilotherm that lives in a thermal environment that varies seasonally must have a means of surviving long periods of temperature outside that range. Warm-adapted species can survive low temperatures in quiescence, but cold-adapted species may need diapause to survive periods of high temperature.

Why are dragonflies less variable than other groups?

Holometabolous development, with its quite separate development of larval and adult characteristics, may facilitate independent temperature responses by different stages. For example, Narang & Narang (1975) showed that each developmental stage of the mosquito *Culex pipiens fasciatus* had a characteristic electrophoretic and gel isoelectric focusing pattern for malate dehydrogenase, and the MDH isozymes from larvae, pupae and adults differed greatly in their response to 50° and 56°C (although these particular temperatures have little ecological relevance). Other examples from

the Diptera show that both evolutionary adaptation and proximal acclimation of responses to temperature can proceed with surprising rapidity (Buffington, 1969; Meats, 1983).

On the other hand, development of each stage in hemimetabolous insects may be constrained by the requirements of the other stages, if genetic control is less sequential than in holometabolous insects. This constraint, coupled with the narrow thermal activity of enzymes, could result in all stages of an hemimetabolous insect responding similarly to temperature. Odonata have very low levels of electrophoretic variation (J.S. Zloty, pers. comm.), and the high temperature requirement of the adult may dominate thermal adaptation. Adult Odonata are long lived and their mating success depends on the ability to make complex aerial manoeuvres and often to spend long periods in flight, activities that they do best in warm conditions, often only in sunshine. Given that adults require high temperatures, it is perhaps unlikely that the eggs they lay would have been selected for cold-tolerance. Why then have the Plecoptera and especially the Odonata's probable sister group, the Ephemeroptera, not been similarly constrained? Probably because adults of these groups do not have such strict temperature requirements. Adult Ephemeroptera are very short-lived and fly under a range of temperatures, whereas adult Plecoptera largely restrict themselves to the ground or tree trunks and fly very little.

Diapause and growth rate are two life-history characteristics of insects that can be modified evolutionarily to synchronize the life-cycle with seasonal changes in the environment (Butler, 1984; Tauber *et al.*, 1986; Danks, 1987). Pritchard (1982) pointed out that Odonata differ markedly from other aquatic insects in their universal adoption of diapause (usually in the larval stage) for seasonal regulation in the north temperate zone. The challenge now is to discover what it is about the evolutionary history of the Odonata that led them to adopt this strategy.

CONCLUDING REMARKS

Our results show that the metabolic responses of aquatic insect eggs to temperature are associated with taxonomy at the ordinal level. This does not necessarily mean that evolution has been constrained by history (Roff, 1992), but it does suggest that different orders have adopted different strategies to deal with the colonization of new thermal habitats. The Odonata appear not to have undergone metabolic changes at all, as all species with eggs that develop directly at favourable temperatures (i.e. excluding species such as some *Lestes*, *Aeshna*, *Sympetrum*, etc. which pass temperate-zone winters as eggs in diapause out of water) have very similar high temperature optima for egg development. Consequently, they lay their eggs into warm water during the summer. The Diptera and Ephemeroptera that we examined are also generally warm-adapted, probably reflecting their origins in warm-water habitats. However, these insects show a greater range of reaction norms than do the Odonata, and one mayfly (*Rhithrogena loyolaea*) is decidedly cold-adapted. Most Plecoptera reflect the cold-water origins of the group, often coupling a cold-adapted metabolism with a graded diapause response which allows them to survive high temperatures at which enzyme function may deteriorate. However, some families of stoneflies have colonized habitats which, at least occasionally, are warm, and many of the species in these families that we examined are now warm-adapted.

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APPENDIX 1

Correspondence of statistics for regressions comparing development time or day-degrees as responses to temperature

For the purposes of this paper, egg development could be measured as either the time between oviposition and hatching (D) at a given temperature (T), or the cumulative temperature sum during this period (day-degrees, DT). If we assume that development is a power function of temperature, then $D = pT^a$ and $DT = aT^b$, which can be log-transformed to linear equations,

$$\log D = \log p + q \log T \quad \text{eqn A1}$$

$$\log D + \log T = \log a + b \log T. \quad \text{eqn A2}$$

This appendix identifies the underlying correspondences between regression statistics for models based on eqn A1 and A2. To simplify terms, we will refer to $\log D$ as Y and $\log T$ as X .

Demonstration of these correspondences requires definition of the variance of $X + Y$ (σ_{X+Y}^2) and the covariance of X and $X + Y$ ($\sigma_{X, X+Y}$). The variance of the sum of two random variables, X and Y , is

$$\sigma_{X+Y}^2 = \sigma_X^2 + \sigma_Y^2 + 2\sigma_{X,Y}, \quad \text{eqn A3}$$

where σ_X^2 and σ_Y^2 are the variances of the two variables and $\sigma_{X,Y}$ is their covariance (Neter *et al.*, 1990). The covariance of two variables is

$$\sigma_{X,Y} = E[XY] - E[X] E[Y],$$

where $E[\]$ represents the expected value (mean) of the quantity in brackets. Therefore

$$\begin{aligned} \sigma_{X, X+Y} &= E[X(X+Y)] - E[X] E[X+Y] \\ &= E[XY] - E[X] E[Y] + E[X^2] - (E[X])^2. \end{aligned} \quad \text{eqn A4}$$

The first two terms in eqn A4 equal $\sigma_{X,Y}$ and the last two terms equal σ_X^2 , so that

$$\sigma_{X, X+Y} = \sigma_{X,Y} + \sigma_X^2. \quad \text{eqn A5}$$

Given eqn A3 and A5, we can compare the regression statistics for the models given by eqn A1 and A2.

q and b — The ordinary least squares estimator for q is $\text{cov}(X,Y)/S_X^2$, where $\text{cov}(X,Y)$ is the sample estimate of the covariance between X and Y , and S_X^2 is the sample estimate of the variance of X (Neter *et al.* 1990). Similarly,

$$b = \text{cov}(X, X+Y)/S_X^2.$$

After incorporating the description for $\text{cov}(X, X+Y)$ given in eqn A5,

$$\begin{aligned} b &= [\text{cov}(X, Y) + S_X^2]/S_X^2 \\ &= q + 1. \end{aligned} \quad \text{eqn A6}$$

$\log p$ and $\log a$ — The ordinary least squares estimator for the regression intercept ($\log p$) is $Y_{\text{mean}} - q X_{\text{mean}}$, where X_{mean} and Y_{mean} are the means for X and Y , respectively (Neter *et al.* 1990). Similarly,

$$\begin{aligned} \log a &= Y_{\text{mean}} + X_{\text{mean}} - b X_{\text{mean}} \\ &= Y_{\text{mean}} - (b-1) X_{\text{mean}} \\ &= Y_{\text{mean}} - q X_{\text{mean}} \\ &= \log p. \end{aligned}$$

Error Mean Square (MS_E) — For the model given by eqn A1,

$$MS_E = \frac{(n-1) [S_Y^2 - q \text{cov}(X, Y)]}{n-2}, \quad \text{eqn A7}$$

The equivalent expression for the model given by eqn A2 is

$$MS_E = \frac{(n-1) [S_X^2 + S_Y^2 + 2\text{cov}(X, Y) - b\{\text{cov}(X, Y) + S_X^2\}]}{n-2},$$

which reduces to eqn A7.

Standard errors for slopes and intercepts

These standard errors are functions of MS_E and the distribution of X , which are identical for the two models. As a result, considering development time or day-degrees does not affect the standard error of the slopes and intercepts. Because of these results and the identity given by eqn A6, statistical comparison of q with a parametric value of 0 provides numerically identical results to comparison of b with a parametric value of 1.

Neter J, Wasserman W, Kutner MH. 1990. *Applied linear statistical models*. 3rd ed. Homewood, IL: Irwin.

APPENDIX 2.

Statistics of the power equation ($DT=aT^b$) relating number of day-degrees (DT) required to complete development by eggs of aquatic insects to temperature (T). The statistics were derived from raw and summarized data in the literature, personal communications, or unpublished data (Ref.). See Methods for more information

Species	r^2 †	a 95% CI*	$b \pm$ 95% CI	P ($H_0: b=0$)	Ref.
PLECOPTERA					
Euholognatha					
Capniidae					
<i>Capnia atra</i> (Lomma)	0.980	240	-0.002±0.142	>0.75	7
<i>C. bifrons</i>	0.957	316	0.000±0.068	>0.75	11
		275–364			
<i>C. gracilaria</i>	0.879	199	0.066±0.261	>0.50	34
		187–212			
<i>C. nana</i>	1.000	107	0.319±0.214	<0.05 ²	34
		64–178			
<i>Mesocapnia oenone</i>	0.987	197	0.409±0.038	<0.001 ²	5
		183–213			
<i>Utacapnia trava</i> (St. M.)	0.815	154	0.134±0.273	>0.25	34
		78–306			
<i>U. trava</i> (Crow's Nest)	0.944	177	0.155±0.145	<0.05 ²	34
		125–252			
Leuctridae					
<i>Leuctra digitata</i>	0.963	340	0.113±0.119	<0.05 ²	27
		268–432			
<i>L. fusca</i>	0.939	289	0.185±0.185	<0.05 ²	27
		248–410			
<i>L. fusca</i>	0.969	279	0.202±0.034	<0.05 ²	12
		258–302			
<i>L. geniculata</i>	0.969	369	-0.035±0.083	>0.05 ²	12
		305–447			
<i>L. hippopus</i>	0.887	120	0.427±0.049	<0.05 ²	12
		107–135			
<i>L. hippopus</i>	0.974	541	-0.189±0.055	<0.001 ¹	30
		475–616			
<i>L. inermis</i>	0.946	145	0.296±0.040	<0.05 ²	12
		132–159			
<i>L. moselyi</i>	0.946	158	0.301±0.074	<0.05 ²	12
		133–188			
<i>L. nigra</i>	0.981	363	-0.006±0.061	>0.05	12
		314–418			
Nemouridae					
<i>Amphinemura banksi</i>	0.005	136	1.026±0.188	<0.001 ²	34
		90–206			
<i>A. standfussi</i>	0.885	281	0.589±0.105	<0.05 ²	13
		229–345			
<i>A. sulcicollis</i>	0.941	60.5	0.548±0.030	<0.05 ²	13
		56.4–64.9			
<i>Malenka californica</i>	0.926	256	0.164±0.166	>0.75	34
		168–390			
<i>Nemoura arctica</i>	0.946	229	0.023±0.119	>0.50	28
		173–302			
<i>N. avicularis</i>	0.971	492	-0.237±0.068	<0.05 ¹	13
		417–582			
<i>N. cambria</i>	0.959	289	0.045±0.050	>0.05	13
		256–327			
<i>N. cinerea</i>	0.906	352	-0.061±0.259	>0.50	6
		203–612			
<i>N. cinerea</i>	0.973	456	-0.246±0.060	<0.05 ¹	13
		389–536			

APPENDIX 2. (Continued)

Species	$r^{2†}$	a 95% CI*	$b \pm$ 95% CI	P ($H_0: b=0$)	Ref.
Euholognatha (continued)					
Nemouridae (continued)					
<i>N. erratica</i>	0.981	356 318–398	-0.019±0.047	>0.05	13
<i>N. viki</i>	0.944	228 169–308	0.003±0.129	>0.75	28
<i>Nemurella pictetii</i>	0.890	270 164–446	-0.060±0.210	>0.50	10
<i>N. pictetii</i>	0.956	296 254–344	-0.127±0.062	<0.05 ¹	13
<i>Protonemura meyeri</i>	0.976	525 465–592	-0.221±0.049	<0.05 ¹	13
<i>P. montana</i>	0.977	336 298–379	-0.020±0.050	>0.05	13
<i>P. praecox</i>	0.891	240 199–289	0.146±0.076	<0.05 ²	13
<i>Zapada cinctipes</i> (Elk)	0.958	198 154–257	0.064±0.100	>0.10	34
<i>Z. cinctipes</i> (BHS)	0.977	202 154–266	0.084±0.114	>0.10	34
<i>Z. columbiana</i>	0.983	197 168–232	0.201±0.074	<0.001 ²	34
Notonemouridae					
<i>Austrocercella alpina</i>	0.914	168 83–340	0.359±0.316	>0.05	3
<i>A. hynesi</i>	0.991	302 263–347	0.026±0.059	>0.25	3
<i>A. illiesi</i>	0.895	227 95–543	0.124±0.387	>0.25	3
<i>A. tillyardi</i>	0.940	288 161–514	0.094±0.250	>0.25	3
Taeniopterygidae					
<i>Taeniopteryx nebulosa</i>	0.988	283 235–339	0.003±0.077	>0.75	2
Systemlognatha					
Perlodidae					
<i>Diura bicaudata</i> (stream)	0.687	383	0.867±0.053	<0.05 ^{2**}	14
<i>D. bicaudata</i> (Lake)	0.982	1885	-0.202±0.052	<0.05 ^{1**}	14
<i>Isogenus nubecula</i>	0.990	571	0.055±0.085	>0.05 ^{**}	14
<i>Isoperla difformis</i>	0.987	2478 1508–4071	-0.628±0.190	<0.001 ¹	42
<i>I. grammatica</i>	0.882	1539 425–5245	-0.369±0.449	>0.05	42
<i>I. obscura</i>	0.173	354 317–394	0.972±0.053	<0.001 ²	42
<i>Perlodes microcephala</i>	0.945	254	0.404±0.041	<0.05 ^{2**}	14
<i>Skwala parallela</i>	0.970	1036 848–1265	-0.306±0.087	<0.001 ¹	34
Perlidae					
<i>Dinocras cephalotes</i>	0.982	2371 1612–3486	-0.402±0.136	<0.001 ¹	29
<i>D. cephalotes</i>	0.927	10219 1616–64589	-0.930±0.753	<0.05 ¹	17
<i>Perla bipunctata</i>	0.996	6483	-0.601±0.024	<0.05 ^{1**}	14

APPENDIX 2. (Continued)

Species	$r^{2\dagger}$	a 95% CI*	$b \pm$ 95% CI	P ($H_0: b=0$)	Ref.
Systemlognatha (continued)					
Chloroperlidae					
<i>Chloroperla tripunctata</i>	0.959	253	0.541±0.021	<0.05 ^{2**}	14
<i>Siphonoperla burmeisteri</i>	0.988	2684	-0.677±0.186	<0.001 ¹	29
		1664–4329			
<i>S. torrentium</i>	0.990	1219	-0.368±0.023	<0.05 ^{1**}	14
ODONATA					
Coenagrionidae					
<i>Argia moesta</i>	0.925	59278	-1.575±0.400	<0.001 ¹	26
		16686–210584			
<i>A. vivida</i> (AC)	0.947	41357	-1.469±0.219	<0.001 ¹	25
		21019–81372			
<i>A. vivida</i> (CB)	0.985	14545	-1.168±0.107	<0.001 ¹	25
		10475–20195			
<i>A. vivida</i> (DC)	0.974	5721	-0.888±0.118	<0.001 ¹	25
		570–8244			
<i>Coenagrion puella</i>	0.997	21764	-1.260±0.124	<0.001 ¹	51
		15084–31400			
<i>Enallagma boreale</i>	0.974	24100	-1.372±0.308	<0.001 ¹	40
		9728–59706			
<i>E. cyathigerum</i>	0.993	26108	-1.404±0.234	<0.001 ¹	39
		13040–52270			
<i>E. ebrium</i>	0.952	68186	-1.606±0.415	<0.001 ¹	36
		18864–246468			
<i>E. hageni</i>	0.964	15522	-1.201±0.231	<0.001 ¹	32
		7716–31221			
<i>E. vernale</i>	0.987	47572	-1.484±0.308	<0.001 ¹	36
		18070–125237			
<i>Ischnura verticalis</i>	0.962	17659	-1.256±0.222	>0.001 ¹	15
		678–90686			
Corduliidae					
<i>Cordulia shurtleffi</i>	0.947	8135	-1.005±0.435	<0.01 ¹	40
		2029–32608			
Libellulidae					
<i>Leucorrhinia borealis</i>	0.988	30333	-1.455±0.498	<0.01 ¹	40
		6508–141377			
<i>L. glacialis</i>	0.979	87553	-1.716±0.455	<0.001 ¹	38
		20397–376736			
<i>L. proxima</i>	0.991	32860	-1.477±0.425	<0.01 ¹	38
		8844–122078			
<i>Libellula julia</i>	0.923	24588	-1.473±0.780	<0.01 ¹	37
		2390–252917			
EPHEMEROPTERA					
Baetidae					
<i>Baetis rhodani</i>	0.991	592	-0.359±0.098	<0.001 ¹	1
		448–782			
<i>Baetis soror</i>	0.993	3213	-0.887±0.179	<0.001 ¹	43
		1955–5282			
<i>Cloeon triangulifer</i>	0.987	40946	-1.694±0.558	<0.01 ¹	46
		7882–212700			
Coloburiscidae					
<i>Coloburiscoides</i> nr <i>haleuticus</i>	0.996	2217	-0.607±0.222	<0.05 ¹	4
		1183–4156			

APPENDIX 2. (Continued)

Species	$r^{2\dagger}$	a 95% CI*	$b \pm$ 95% CI	P ($H_0: b=0$)	Ref.
Ecdyonuridae					
<i>Ecdyonurus dispar</i> (Wind.)	>0.97	3242 2724–3858	–0.810±0.070	<0.001 ¹	21
<i>E. dispar</i> (Enn)	>0.97	3218 2704–3829	–0.760±0.120	<0.001 ¹	21
<i>E. insignis</i>	>0.97	7881 6567–9597	–1.220±0.070	<0.001 ¹	21
<i>E. picteti</i> (Herrn)	>0.97	1655 1346–2036	–0.470±0.090	<0.001 ¹	21
<i>E. picteti</i> (Seebach)	>0.97	1227 1076–1399	–0.470±0.060	<0.001 ¹	21
<i>E. picteti</i> (unfert.)	0.98	1610 1175–2206	–0.330±0.130	<0.001 ¹	22
<i>E. torrentis</i>	>0.97	2610 1992–3419	–0.820±0.110	<0.001 ¹	21
<i>E. torrentis</i> (unfert.)	0.98	2943 1863–4650	–0.710±0.190	<0.001 ¹	22
<i>E. venosus</i> (Brathay)	>0.97	3516 3005–4114	–0.900±0.060	<0.001 ¹	21
<i>E. venosus</i> (Seebach)	>0.97	2593 2235–3008	–0.680±0.060	<0.001 ¹	21
<i>E. venosus</i> (fluct. temp.)	>0.97	3492 2512–4854	–0.810±0.150	<0.001 ¹	23
<i>E. venosus</i> (unfert.)	0.92	3026 1081–8473	–0.450±0.410	<0.05 ¹	22
EphemereIIDae					
<i>Ephemerella funeralis</i> (first hatch)	0.959	1513 127–17935	–0.398±0.875	>0.10	45
<i>E. subvaria</i> (first hatch)	0.986	3748 719–19545	–0.604±0.584	<0.05 ¹	45
Ephemeridae					
<i>Hexagenia bilineata</i>	0.990	341123 16450–7073697	–2.199±0.981	<0.05 ¹	52
<i>H. rigida</i> (first hatch)	0.954	23624 2605–214267	–1.373±0.721	<0.01 ¹	16
Euthypocidae					
<i>Euthyplocia hecuba</i>	1.00	101722 94750–109758	–1.520±0.006	<0.01 ¹	47
Heptageniidae					
<i>Rhithrogena cf. hybrida</i>	>0.98	892 743–1070	–0.330±0.080	<0.001 ¹	24
<i>R. loyolae</i>	0.75	297 280–315	0.760±0.040	<0.001 ²	24
<i>R. semicolorata</i> (Wilf)	>0.98	3481 3053–3968	–0.930±0.050	<0.001 ¹	24
<i>R. semicolorata</i> (Lune)	>0.98	3020 2157–4228	–0.870±0.130	<0.001 ¹	24
Leptophlebiidae					
<i>Nousia fuscula</i>	1.00	2760 1786–4266	–0.670±0.170	<0.001 ¹	43
<i>N. inconspicua</i>	0.85	4180 207–84198	–0.860±0.870	>0.05	43
Siphonuridae					
<i>Isonychia bicolor</i> (fluct.temp.)	0.962	5198 771–35039	–0.860±0.728	<0.05 ¹	44

APPENDIX 2. (Continued)

Species	r^{\dagger}	a 95% CI*	$b \pm$ 95% CI	P ($H_0: b=0$)	Ref.
Tricorythidae					
<i>Tricorythodes minutus</i>	0.929	988 426–2295	0.000±0.842	>0.75	35
DIPTERA					
Culicidae					
<i>Aedes aegypti</i>	0.959	95030 1407–6417782	-2.124±1.338	<0.05 ¹	9
<i>Ae. sticticus</i>	0.836	645 221–1885	-0.446±0.363	<0.05 ¹	50
<i>Ae. vexans</i>	0.985	2063 1069–3982	-0.995±0.218	<0.001 ¹	19
<i>Anopheles quadrimaculatus</i>	0.983	4591 2456–8585	-1.371±0.121	<0.001 ¹	20
<i>Culex pipiens</i> (first hatch)	0.940	1607 490–5272	-1.137±0.399	<0.01 ¹	41
<i>Cx. pipiens</i>	0.834	175 78–391	-0.424±0.263	<0.05 ¹	31
<i>Cx. restuans</i>	0.956	349 92–1325	-0.673±0.438	<0.05 ¹	31
<i>Cx. annulirostris</i>	0.836	262 28–2459	-0.503±0.679	>0.05	33
<i>Toxorhynchites brevipalpis</i>	0.952	9063 4638–17708	-1.641±0.221	<0.001 ¹	49
<i>Tx. rutilus</i> (Delaware)	0.997	2131	-1.111± ?		48
<i>Tx. rutilus</i> (Louisiana)	0.993	1595	-1.039± ?		48
Tipulidae					
<i>Tipula commiscibilis</i>	0.989	486 400–590	-0.422±0.073	<0.001 ¹	39
<i>Tipula maxima</i>	0.999	798 619–1028	-0.565±0.089	<0.01 ¹	8
Sciomyzidae					
<i>Ilione albiseta</i>	0.602	177 54–581	0.618±0.430	<0.05 ²	18
<i>Limnia unguicornis</i>	0.679	116 18–747	0.506±0.624	>0.05	18
<i>Pherbellia cinerella</i>	0.666	989 2–402164	-0.551±2.015	>0.25	18

¹ $=b$ significantly below zero. ² $=b$ significantly above zero.

[†] $=r^2$ from equation relating days to temperature.

* confidence interval for a is back-transformed from logarithm.

** probability estimated from confidence intervals.

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