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A general rule for the dependence of developmental rate on temperature in ectothermic animals

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In animals that do not regulate their body temperature by the production of heat, the proportion of the total developmental time spent in a particular developmental stage does not change with temperature. In the quasi-linear region of the relationship between developmental rate and temperature, all of the developmental stages appear to have the same species-specific lower developmental threshold. This trait, which is called developmental isomorphy, constrains developmental adaptations of ectotherms to their environments and facilitates the precise timing of life-history events.

Keywords: developmental time; thermal requirements; lower development threshold; rate isomorphy; developmental constraints; life-history characteristics

1. INTRODUCTION

Ectotherms, i.e. plants, fungi, protists and all animals except birds and mammals, rely on external sources of heat. The ambient temperature determines the developmental rate (DR) of ectotherms, i.e. development is slower at low than at high temperatures. A general model recently derived by Gillooly *et al.* (2002) predicts that developmental time in animals is a function of body mass and temperature. However, an intraspecific model for predicting developmental events at different temperatures should not assume a close connection between growth and differentiation, but be based only on differentiation rate (Smith-Gill & Berven 1979). Development can be thought of as consisting of two different components: differentiation and development (diversification of cell types), and growth (increase in biomass), which are only loosely connected (Van der Have & de Jong 1996). For example, growth is not coupled with early differentiation in many animals (e.g. amphibians) or to development during non-feeding stages in insects (e.g. pupa). Another example, which indicates that growth and differentiation are driven by different and functionally separate mechanisms, is the well-documented effect of temperature on size in ectotherms (Atkinson 1994; Atkinson & Sibly 1997) (referred to as a 'major life-history puzzle'). That is, many organisms mature later and at a larger size at low than at high temperatures when food is supplied *ad libitum*. Over a range of 15 °C body size can change by *ca*. 30% (Voorhies 1996), which is biologically relevant as body size is central to many life-history traits (Stearns 1992). However, Gillooly *et al.* (2002) assumes that rearing temperature does not affect final weight.

Van der Have & de Jong (1996) and Dettlaff (2001) assume that a basic process regulates the timing of major developmental events. They suggested that the rate of differentiation is determined primarily by cell division, i.e. an increase in cell number during development. Specifically, the duration of cell division should be the key process regulating differentiation rate. This approach predicts that the duration of all the developmental stages should be equally affected by temperature. Consequently, the proportion of the total developmental time spent in a particular developmental stage should not change with temperature. This was recently shown for non-dormant (i.e. non-diapaused) populations of insects ($n = 417$) and mites ($n = 9$) (Jarošík *et al.* 2002). Here, this analysis is extended to 22 representatives of other groups of animals (especially vertebrates, but also other invertebrate groups; see the data in electronic Appendix A, available on The Royal Society's Publications Web site), which do not regulate their temperature by the production of body heat. In non-arthropod taxa, the timing of developmental events is based on the time of appearance of morphological markers characteristic of a given stage. For arthropods, we used the time of moulting as an indicator of the duration of a particular stage, which is theoretically well founded: moulting is a hormone-stimulated process determined primarily by the stage of differentiation reached (Holliday 1991).

2. METHODS

The proportionality in duration of non-dormant developmental stages of a species reared at a range of constant temperatures was tested using meta-analysis, a statistical synthesis of the results of separate independent experiments. The angular transformed proportion of total developmental time spent in a particular stage of a population of a species was plotted against temperature and tested following Jarošík *et al.* (2002). The existence of developmental isomorphy was inferred from a zero change in the regression coefficient of this relationship (see table 2 in electronic Appendix A). All studies, including those previously analysed for insects and mites (Jarošík *et al.* 2002), were grouped taxonomically, and the outcome of each analysis represented by a quantitative index of the effect size, independent of sample size and the scale of measurement of the population of the species. Following Rosenthal (1994), the cumulative effect size across studies within each group was determined using the regression coefficients of the relationships between transformed proportions and temperature. The absolute value of the largest regression slope from each analysis was used (because a change in the proportion of the time spent in one stage changes inversely the other proportions), and the null hypothesis that the overall effect size indicates a zero slope was tested as a one-sided hypothesis. The null hypotheses that (i) the cumulative effect size across a group is zero; (ii) all the individual analyses within a group share a common population effect size; and (iii) there are no differences between the groups, were tested following Gurevitch & Hedges (2001), Shadish & Haddock (1994) and Hedges (1994).

3. RESULTS AND DISCUSSION

This meta-analysis revealed the ubiquity of the predicted proportionality in ectotherm development (table 1). The existence of developmental proportionality has important evolutionary and practical implications. First, from an evolutionary point of view, developmental

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Table 1. The cumulative effect sizes, their 95% confidence intervals (CI), the test statistics of the null hypothesis on developmental proportionality (Z) and the homogeneity of the effect sizes (Q).

(The proportional time spent in a stage does not vary with temperature: specifically, the CIs of effect sizes include zero, and therefore the null hypotheses, Z, that the overall cumulative effect sizes are zero cannot be rejected. All the analyses share a common population effect size, indicating developmental proportionality, because the observed variances in effect sizes, Q, of individual groups of taxa are not significantly greater than expected by chance, and all effect sizes are equal ($Q_{\text{between groups}} = 0.215$, d.f. = 3, $p = 0.97$).)

group	effect size	95% CI	Z	p	Q	d.f.	p
insects and mites	0.000135	−0.000251–0.000520	0.57	0.71	4.250	422	1
other invertebrates	0.00760	−0.0795–0.0947	0.14	0.56	0.000143	1	0.99
fishes	0.00421	−0.0140–0.0224	0.38	0.65	0.240	9	1
amphibians	0.00173	−0.00900–0.0125	0.26	0.60	0.0728	9	1
grand total	0.000139	−0.000247–0.000524	0.59	0.72	4.563	441	1

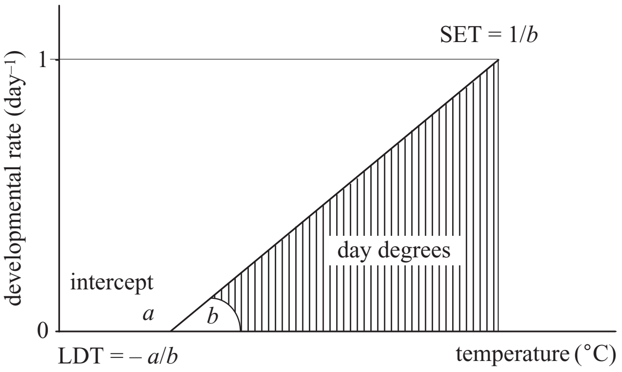

Figure 1. The linear relationship between the DR (i.e. proportion of development occurring per unit time) and temperature, t, over a range of ecologically relevant temperatures. The relationship between DR and t can be described as DR = $a + bt$, where a is the intercept with the y-axis, and b is the slope of the linear function. From this equation the LDT can be estimated as LDT = $-a/b$. Graphically, LDT is the value at which the relationship intercepts the temperature axis. Using the relationship between DR and t, the SET, i.e. number of day degrees above the LDT necessary for the completion of a particular developmental stage (DR = 1, t = SET, $a = 0$) can also be estimated: SET = $1/b$.

isomorphy probably constrains the evolution of life-history strategies in ectotherms. The fact that all of the developmental stages of a species have a common developmental threshold means that selection on a particular developmental stage, independent of other developmental stages, is constrained (cf. Trudgill 1995; Gilbert & Raworth 1996; Jockusch 1997; Lamb 1988; Charnov & Gillooly 2003). That is, a particular stage cannot adapt to the temperature of its environment without affecting the thermal adaptation of all of the other developmental stages.

Second, it simplifies the timing of life-history events and the determination of thermal requirements, which is important, for example, when forecasting and monitoring pests (Campbell *et al.* 1974). The linear approximation of the relationship between the differentiation rate (the reciprocal of the duration of development) and temperature, widely used in practical applications, enables the calculation of two virtual constants: the sum of effective temperatures (SET), the amount of heat needed for completing a developmental stage, and the lower developmental threshold (LDT), the temperature below which development ceases (figure 1). A linear approximation gives the most appropriate fit within the quasi-linear region of the relationship (i.e. where the temperatures are ecologically relevant) (Wagner *et al.* 1984; Honěk & Kocourek 1988, 1990; Charnov & Gillooly 2003). That the same proportion of the total time is spent in a particular developmental stage at different temperatures implies that the LDT is the same for all developmental stages of a population of a species, i.e. an organism shows a trait called developmental isomorphy (figure 1; Jarošík *et al.* 2002). Thus, LDT can be established for a stage, for example the developmental time of the pupa of an insect, in which the effect of factors other than temperature is minimal, and the SET may be calculated from the duration of development at only one temperature. The saving in experimental work can be invested in a more precise determination of the length of development.

Last but not least, our findings support Dettlaff's notion (Dettlaff 2001) that the duration of a cell cycle, which is strongly affected, for example, by the genome size of a particular organism (Jockusch 1997; Gregory 2001), could serve as a biological time clock for animal development at different temperatures.

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