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Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling

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ABSTRACT

The developmental response of insects to temperature is important in understanding the ecology of insect life histories. Temperature-dependent phenology models permit examination of the impacts of temperature on the geographical distributions, population dynamics and management of insects. The measurement of insect developmental, survival and reproductive responses to temperature poses practical challenges because of their modality, variability among individuals and high mortality near the lower and upper threshold temperatures. We address this challenge with an integrated approach to the design of experiments and analysis of data based on maximum likelihood. This approach expands, simplifies and unifies the analysis of laboratory data parameterizing the thermal responses of insects in particular and poikilotherms in general. This approach allows the use of censored observations (records of surviving individuals that have not completed development after a certain time) and accommodates observations from temperature transfer treatments in which individuals pass only a portion of their development at an extreme (near-threshold) temperature and are then placed in optimal conditions to complete their development with a higher rate of survival. Results obtained from this approach are directly applicable to individual-based modeling of insect development, survival and reproduction with respect to temperature. This approach makes possible the development of process-based phenology models that are based on optimal use of available information, and will aid in the development of powerful tools for analyzing eruptive insect population behavior and response to changing climatic conditions.

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1. Introduction

The physiological responses of organisms to temperature have had considerable attention in the scientific literature for more than a century. Recently, debate focused on a Metabolic Theory of Ecology (MTE) where temperature and body weight are the fundamental determinants of the rates at which life's central processes occur: metabolism, development, reproduction, population growth, species diversity and even ecosystem processes (Brown et al., 2004). Discussion centers around the existence of a Universal Temperature Dependence (UTD), in the form of the exponential Arrhenius equation $r = b_0 \exp(-E/kT)$ where r is some rate, b_0 is a proportionality constant that varies between processes and taxa, $E \approx 0.6$ to 0.7 eVK⁻¹ is a near-constant activation energy, and $k = 8.6173 \times 10^{-5}$ eVK⁻¹ is the Boltzmann constant relating energy

to temperature, K (°K). Arguments have centered on the validity and universality of the UTD (Clarke, 2006; Clarke and Fraser, 2004; Huey and Kingsolver, 2011) and the constancy and ecological correlates of its main parameter E (Dell et al., 2011; Irlich et al., 2009). The UTD provides an adequate description of biological rate responses over a limited range of temperatures but over the range of temperatures to which poikilotherms such as insects are exposed, responses to temperature are unimodal (Sharpe and DeMichele, 1977; Knies and Kingsolver, 2010). Consequently, the breadth of temperature range, thresholds and optimum temperatures at which this unimodality is expressed, as well as their variability are critical (Angilletta et al., 2002; de Jong and van der Have, 2009; Dixon et al., 2009).

For cold-blooded organisms, including insects, the relationships between ambient temperature and development, survival and reproduction scale up from daily or even hourly effects on individuals to seasonal patterns of phenology (Schwartz, 1998; Visser and Both, 2005), population dynamics (Logan et al., 2006; Yang and Rudolf, 2010), and species distributions including the expanding

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interest in responses to climate change (Bentz et al., 2010; Kramer et al., 2000; Powell and Logan, 2005; Régnière and Logan, 2003; Sparks and Carey, 1995). Models that aim to predict the effects of temperature on the outcomes of these processes must account for the nonlinear nature of the thermal responses involved (Régnière and Logan, 2003; Schaalge and van der Vaart, 1988; Smerage, 1988), as well as the intraspecific and intrapopulation variability in these responses.

The intrinsic variability of developmental rates among individuals within populations (*sensu* Yurk and Powell, 2010) influences the observed distribution of phenological events in those populations. Thermal responses are often asymmetrically distributed and as such they can alter the timing of life stages (Gilbert et al., 2004) and its demographic consequences (Bellows, 1986; Powell and Bentz, 2009). From mathematical descriptions of these distributions, simulation models can generate age or stage frequencies including survival and reproduction over time in response to temperature input regimes. The most commonly used model categories are distributed delays (Manetsch, 1976), cohort-based (Sharpe et al., 1977), and individual-based (Cooke and Régnière, 1996; DeAngelis and Gross, 1992; Grimm, 2008).

Three issues in the design and analysis of temperature response experiments used to estimate parameters of phenology models are: (1) analysis of development times or their inverse, development rates (Kramer et al., 1991); (2) estimation of development times at temperatures near thresholds (extremes) where excessive mortality or developmental abnormalities such as the inability to hatch from an egg may occur; and (3) the relationship between individual variation and average developmental rates (Régnière, 1984; Wagner et al., 1984) and reproductive responses (Régnière, 1983).

In this paper, we propose a formal methodological framework within which to design experiments and analyze data on insect development, survival and reproduction responses estimated from individuals observed living in controlled, but not necessarily constant, temperatures. Our framework allows: (1) the use of censored data, where observations are interrupted after a certain time; (2) parsing of variance contributions between individual (intrinsic) and lack-of-fit; and (3) more precise estimation of thresholds by the transfer of individuals between extreme and moderate temperatures. It expands, simplifies and unifies the analysis of laboratory data parameterizing the thermal responses of insects in particular and poikilotherms in general. We demonstrate this approach using simulated data, data from the literature on the eastern spruce budworm *Choristoneura fumiferana* (Clem.), the spruce budmoth *Zeiraphera canadensis* Nutt. and Freeman (Lepidoptera: Tortricidae), the melon fly *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), as well as new data from the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), Scolytinae) and the western spruce budworm *C. occidentalis* Freeman (Lepidoptera: Tortricidae).

2. Theory

2.1. Rate-summation models of insect development

The development rates of insects are rarely measured directly. Instead, they are calculated as the inverse of observed development time, such as the number of days between oviposition and hatch or between successive larval moults, and are expressed as proportions of total stage duration per unit of time. Development time and rate are related by:

$$\tau(T, \mathbf{A}) = \frac{1}{r(T, \mathbf{A})}, \quad (1)$$

where $\tau(T, \mathbf{A})$ represents the modeled average time required to complete the life stage at temperature T , and \mathbf{A} is a vector of parameter

values of temperature-response function $r(T, \mathbf{A})$. To model development under fluctuating temperature regimes, it is necessary to sum (integrate) development rates over short time steps, Δt , usually of a day or less (Régnière and Logan, 2003). This sum represents within-stage physiological age, a (proportion of the stage completed, from 0 at the onset to 1 at completion):

$$a_t = \int_0^t r(T_t, \mathbf{A}) dt \cong \sum_0^t r(T_t, \mathbf{A}) \Delta t. \quad (2)$$

As defined here, a is analogous to the physiological time scale defined by van Straalen (1983) under the assumption of linear development responses (see de Jong and van der Have, 2009).

2.2. Developmental responses to temperature and distributions

Many functions describe the developmental responses of insects to temperature. They can be classified in order of complexity, as represented by the number of parameters required. Seven functions are described in Table 1 (hereafter referred to as (A1)–(A7)). Of these, the Sharpe–Schoolfield model (A7) (Sharpe and DeMichele, 1977; Schoolfield et al., 1981) is the most “mechanistic” as it is based on enzyme kinetics. It is related to the UTD as it incorporates the Arrhenius equation (see De Jong and van der Have, 2009). Many of the other functions in Table 1 are simpler empirical mathematical descriptions of the shape of the temperature responses without a true mechanistic basis.

Let t_{ij} represent the development time of individual i in t_{ij} treatment j at constant temperature T . Index j could be a temperature treatment, replicate, sub-population, or some other sample unit of the experimental design. There are two sources of variation that make $t_{ij} \neq \tau(T, \mathbf{A})$. First, individuals vary in their responses to temperature. Second, additional sources of variation are pooled together as lack-of-fit between the theoretical thermal response, $\tau(T, \mathbf{A})$, and the true mean (or expected) development time, $E(t_{ij})$. If we define an individual's deviation from $E(t_{ij})$ as δ_{ij} , and the lack-of-fit between theoretical response and treatment mean, v_j , we get:

$$t_{ij} = \delta_{ij} v_j \tau(T, \mathbf{A}). \quad (3)$$

This formulation assumes that the distribution of development time among individuals does not vary with temperature but that its variance is proportional to the square of the mean. Various functions have been used to describe this distribution based on their flexibility or simplicity (Dangles et al., 2008; Régnière, 1984; Stinner et al., 1975; Wagner et al., 1984; Yurk and Powell, 2010). We favor the lognormal distribution for three reasons. It ensures that $\delta \geq 0$, which is consistent with the fact that rates can only be ≥ 0 in all individuals at all temperatures (development cannot regress). It is asymmetrical with a more or less pronounced positive skew (longer right-hand tail), which is a characteristic often observed in the distributions of both development times and development rates in insects (Curry et al., 1978). And it can be inverted without consequence (if ε is normally-distributed then $\delta = e^\varepsilon$ and $1/\delta = e^{-\varepsilon}$ are both lognormally-distributed), the error structure is the same whether variability is expressed as development times or development rates. Thus:

$$\varepsilon_{ij} = \ln\{t_{ij}/[v_j \tau(T, \mathbf{A})]\}, \quad (4)$$

is a normally-distributed random variable with mean $\mu_\varepsilon = -1/2\sigma_\varepsilon^2$ and variance σ_ε^2 (the skew of the lognormal distribution requires a non-zero μ_ε so that $E(\delta_{ij}) = 1$; Hilborn and Mangel, 1997). Because it is based on an expected value (a mean), the lack-of-fit term,

$$v_j = E(t_{ij})/\tau(T, \mathbf{A}), \quad (5)$$

can be assumed to be a multiplicative normally-distributed random effect with mean 1 and variance σ_v^2 that is random with respect to treatment.

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