

# Applying developmental threshold models to evolutionary ecology

Kathleen Donohue<sup>1</sup>, Liana T. Burghardt<sup>1</sup>, Daniel Runcie<sup>2</sup>, Kent J. Bradford<sup>3</sup>, and Johanna Schmitt<sup>2</sup>

<sup>1</sup> Duke University, Department of Biology, Box 90338, Durham, NC 27708, USA

<sup>2</sup> Department of Evolution and Ecology, University of California, Davis, CA 95616, USA

<sup>3</sup> Department of Plant Sciences, University of California, Davis, CA 95616, USA

**Process-based models of development predict developmental rates and phenology as a function of physiological responses to multiple dynamic environmental factors. These models can be adapted to analyze diverse processes in evolutionary ecology. By linking models across life stages, they can predict life cycles and generation times. By incorporating fitness, they can identify environmental and physiological factors that limit species distributions. By incorporating population variance, they can investigate mechanisms of intraspecific variation or synchronization. By incorporating genetics, they can predict genotype-specific phenology under diverse climatic scenarios and examine causes and consequences of pleiotropy across life stages. With further development, they have the potential to predict genotype-specific ranges and identify key genes involved in determining phenology and fitness in variable and changing environments.**

## Modeling phenology to understand evolutionary ecology

Changes in phenology (the timing of developmental events; see [Glossary](#)) in response to changing climate are widely observed and can have critical consequences for organismal fitness and population performance [1–5]. Phenology determines which life stages are exposed to which seasonal conditions and thus can strongly affect life-history expression, generation time, and population dynamics. Predicting phenological responses to different climatic environments is therefore important for understanding how organisms, populations, and species will respond to future climate change.

Process-based developmental models are powerful tools for predicting phenology under complex natural conditions (e.g., [6–17]). Such models use dynamic environmental inputs to predict developmental rates and the timing of phenological transitions. Historically they have been employed primarily in agronomic applications or ecological projections of important events such as bud break or insect emergence dates. However, such models also have potential

to provide insight into diverse ecological and evolutionary processes, including species range limits, phenotypic plasticity in response to complex dynamic environments, and causes of phenotypic and genetic variation within and among populations.

Here we discuss some potential applications of these models to evolutionary ecology. First, we describe how

## Glossary

**Canalization:** the process of reducing variation; for example, among individuals in a population with respect to phenotypes that they express. For phenological traits, this can manifest as synchronization in developmental times.

**Developmental threshold:** the accumulated amount of ‘developmental time’ required for a given developmental stage to allow a transition to the next developmental stage. The time required is in developmental units (e.g., thermal time, degree days) rather than in calendar time units. Once a threshold level of developmental time has accumulated, the developmental transition occurs.

**Developmental threshold model:** a model used to predict the timing of a developmental transition. The timing of developmental transitions from one state to the next is modeled as a function of dynamic environmental factors that influence the accumulation of developmental time (see developmental threshold). Once a threshold level of developmental time has accumulated, the developmental transition occurs.

**Habitat selection:** the ability of an organism to determine (select or choose) the environment that it is exposed to.

**Heritability:** the proportion of total phenotypic variance that is genetic variance (i.e., caused by genetically based differences in phenotypes); total phenotypic variance includes both genetic and environmental variance. Higher heritability enables larger responses to selection, for any given strength of selection.

**Maternal effects:** also termed ‘maternal environmental effects’. The influence of the environment experienced by maternal parents on the phenotype of their offspring.

**Phenology:** the timing of biological events such as germination, flowering, and bud break in plants or hatching, metamorphosis, and reproduction in animals.

**Population-based threshold models (PBTMs):** developmental threshold models that incorporate variation among individuals in a population with respect to developmental responses to environmental (or other) inputs.

**Pleiotropy:** the phenomenon in which one gene regulates more than one trait.

**Process-based model:** a model describing how a physiological process responds to environmental factors that is often used to predict developmental outcomes.

**Quantal:** a quantal response or trait is discontinuous and transitions from one discrete state to another; for example, from non-germinated to germinated or vegetative to reproductive. The phenotypes of quantal traits are frequently expressed as the percentage or proportion of individuals completing the developmental transition.

**Reaction norm:** the function that describes how a single genotype alters its phenotype in response to the environment.

**Sensitivity threshold:** the lower limit of a regulatory signal (environmental, hormonal, biochemical) that elicits a phenotypic response in an organism. When the signal level exceeds the threshold sensitivity, developmental time can accumulate. Sensitivity thresholds are physiologically determined and can be increased or decreased in response to environmental signals or developmental transitions and can vary among individuals.

Corresponding authors: Donohue, K. ([k.donohue@duke.edu](mailto:k.donohue@duke.edu)); Burghardt, L.T. ([liana.burghardt@gmail.com](mailto:liana.burghardt@gmail.com)).

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process-based developmental models, and developmental threshold models in particular, predict the timing of developmental transitions in complex environments and discuss how linking models of multiple life stages across the life cycle captures important dynamics in life cycle expression. Next, we discuss how further development of these models makes them applicable to addressing important issues in evolutionary ecology, specifically by incorporating fitness, population variance, and genetic differences among individuals.

### Developmental threshold models: predicting phenology and life cycles in complex environments

Developmental threshold models predict the rate of development from one life stage to another, given a sequence of environmental conditions (Box 1). ‘Developmental units’ accrue over time according to relationships that describe developmental rate as a function of sensitivities to environmental factors. The effects of multiple environmental factors can be combined to define the rate of accumulation of developmental units. Once a threshold number of developmental units is attained, the developmental transition occurs; for example, the transition from seed to germinant or from egg to larva. This is an extremely flexible framework for predicting phenology in dynamic, complex environments. These and other models of phenology and developmental rates (e.g., [1,18,19]) have been successful in predicting the timing of phenological transitions, developmental rates, and growth rates more generally.

Individual developmental threshold models predict the timing of a single developmental transition. Linking multiple models of developmental transitions throughout the life cycle allows predictions of overall life cycle expression and the total amount of time required to complete a life cycle, or the generation time. Generation time is demographically important because it determines the number of generations that can be completed within a growing season and therefore influences population growth rate.

Linking individual developmental threshold models across the life cycle also incorporates an important dynamic that occurs in organisms developing in the wild: the timing of prior life-stage transitions determines the environmental conditions experienced by subsequent life stages, both within and across generations [20]. Environmentally cued phenology thereby acts as a form of habitat selection (Figure 1A), leading to important effects of one life stage on the following stages because the environment determined by one life stage affects the phenotypes expressed subsequently.

Linked developmental models incorporate these dynamics directly. They have been applied to predict bud break and fruit-maturation timing in trees [21], reproductive timing in crops [22,23], overall life cycle expression in annual plants [24], and the number of insect generations completed per season [25]. These models illustrate why accurate predictions of phenology and total generation time can be made only by incorporating the effects of the phenology of prior life stages on the environmental conditions that are experienced by subsequent ones. For instance, an empirically validated photothermal model [26] showed that flowering time and the expression of

summer annual, winter annual, or autumn-flowering life histories depends critically on the seasonal timing of germination because germination time determined the amount of time before winter temperatures became prohibitive for further development.

The opportunity also exists to model cross-generational influences of maternal environmental effects by linking life stages across generations. The timing of reproduction determines the environmental conditions experienced during embryo development as well as the conditions that progeny are born or dispersed into. Maternal effects are known empirically to influence the expression of plant life histories [27,28], insect egg size and thereby growth rates [29], and even the demography of pest outbreaks ([30]; reviewed in [31]). They can be incorporated into developmental threshold models by allowing the progeny’s developmental parameters to be defined as a function of maternal environmental factors.

Linked developmental threshold models can be used to predict overall life cycle expression across a geographical range or in novel climatic conditions. For example, Burghardt *et al.* [24] linked models of the timing of germination, flowering, and dispersal of *Arabidopsis thaliana* to show how the dynamics of all three processes contribute to the generation time and life-history variation that has been observed across its native range (Figure 1B,C) [24]. Wilczek *et al.* [32] predicted seasonal shifts in the flowering phenology of *A. thaliana* as a function of germination time across the species range under future climatic conditions.

Sensitivity analysis of these models can identify key physiological parameters that have the largest effect on phenology and life cycles (Box 2). For example, Burghardt *et al.* [24] found that changes in the seed dormancy of *A. thaliana* had larger projected effects on generation time than did changes in parameters affecting flowering time, based on a range of parameters known to occur in that species. Sensitivity analyses can also identify key environmental factors with the largest effect for any given set of physiological parameters (individual or genotype). For instance, Andreini *et al.* [33] found that early-flowering cultivars of fruit trees are most impacted by daily minimum temperatures because of their chilling requirement for bud dormancy release, while later-flowering cultivars are influenced primarily by daily mean temperatures.

In summary, developmental threshold models can be linked across the life cycle and across generations to predict integrated life cycle expression in complex environments, capture the important dynamics of habitat selection via developmental cuing and of maternal environmental effects, and project the expression of life cycles and generation times across present ranges and future climatic scenarios. When combined with sensitivity analysis, the models provide testable predictions about which physiological processes or environmental factors are most influential on life-history expression.

### Incorporating fitness to predict species ranges

A crucial step toward adapting developmental and phenological models to applications in evolutionary ecology is to incorporate fitness consequences of developmental timing. Models that predict the seasonal timing of each life stage

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