Modeling the Effects of Developmental Variation on Insect Phenology

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Abstract  Phenology, the timing of developmental events such as oviposition or pupation, is highly dependent on temperature; since insects are ectotherms, the time it takes them to complete a life stage (development time) depends on the temperatures they experience. This dependence varies within and between populations due to variation among individuals that is fixed within a life stage (giving rise to what we call persistent variation) and variation from random effects within a life stage (giving rise to what we call random variation). It is important to understand how both types of variation affect phenology if we are to predict the effects of climate change on insect populations.

We present three nested phenology models incorporating increasing levels of variation. First, we derive an advection equation to describe the temperature-dependent development of a population with no variation in development time. This model is extended to incorporate persistent variation by introducing a developmental phenotype that varies within a population, yielding a phenotype-dependent advection equation. This is further extended by including a diffusion term describing random variation in a phenotype-dependent Fokker–Planck development equation. These models are also novel because they are formulated in terms of development time rather than developmental rate; development time can be measured directly in the laboratory, whereas developmental rate is calculated by transforming laboratory data. We fit the phenology models to development time data for mountain pine beetles (MPB) (\textit{Dendroctonus ponderosae} Hopkins [Coleoptera: Scolytidae]) held at constant temperatures in laboratory experiments. The nested models are parameterized using a maximum likelihood approach. The results of the parameterization show that the phenotype-dependent advection model provides the best fit to laboratory data, suggesting that MPB phenology may be adequately described in terms of persistent variation alone. MPB phenology is simulated using phloem temperatures and attack time distributions measured in central Idaho. The resulting emergence time distributions compare favorably to field observations.

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1. Introduction

Describing variation in the link between temperature and insect phenology (the timing of developmental events such as oviposition, or adult emergence) is a crucial step toward predicting how insect populations will respond to climate change. The time required for an insect to complete a life stage (development time) depends on its thermal environment (Zaslavski, 1988); this response varies within and between populations (Bentz et al., 2001). Variation in development time arises from differences between individuals that are fixed within a life stage (giving rise to what we call persistent variation) as well as from random effects that vary within a life stage (giving rise to what we call random variation). For example, persistent variation incorporates variation in development time due to genetic differences between individuals (assuming an individual’s genotype does not change during a life stage). It also incorporates variation due to persistent environmental effects (e.g., resource quality) or due to maternal effects (e.g., egg size at oviposition). On the other hand, random variation incorporates factors that vary within a life stage, for example, random temperature fluctuations and variation in microhabitat.

Predicting how climate change will affect insect phenology must take both types of variation into account. In particular, it is important to account for persistent variation (which includes the effects of genetic variation) if we are to understand how populations might evolve to cope with climate change (Yurk and Powell, 2009). In this paper, we present three phenology models incorporating increasing amounts of developmental variation, while explicitly separating persistent and random variation. These models are fit to data from constant temperature laboratory experiments for mountain pine beetles (MPB), Dendroctonus ponderosae Hopkins [Coleoptera: Scolytidae], an economically important outbreak insect. The parameterized models are used to simulate MPB phenology using temperatures measured in the field, and phenology predictions are compared to field observations.

The response of insect populations to global warming has been the focus of many recent studies, e.g., Carroll et al. (2003), Logan and Powell (2001), Memmott et al. (2007), Parmesan and Yohe (2003), Visser and Holleman (2001). Temperature change has been linked to shifting phenology (Parmesan and Yohe, 2003) and range expansion (e.g., Carroll et al., 2003) in several natural populations. Insect fitness is highly dependent on phenology; development must be timed to coincide with favorable weather conditions and resource availability. In some populations, development must also be synchronized; synchronous emergence improves mating chances in small populations, reduces per-capita risk of predation, and, in the case of MPB, is necessary to overwhelm defended host trees (Berryman et al., 1985). Since temperature change shifts phenology, global warming will result in strong selection on development time. Predicting how populations might evolve to cope with global warming requires a mechanistic understanding of how phenology depends on temperature before the evolution of that dependence can be modeled.

The work presented here is largely motivated by the need to understand how MPB phenology depends on temperature, how that dependence varies within a population, and how it might adapt to climate change. The MPB is an eruptive bark beetle found in western