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Insect seasonality: circle map analysis of temperature-driven life cycles

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Abstract

Maintaining an adaptive seasonality, with life cycle events occurring at appropriate times of year and in synchrony with cohorts and ephemeral resources, is a basic ecological requisite for many cold-blooded organisms. There are many mechanisms for synchronizing developmental milestones, such as egg laying (oviposition), egg hatching, cocoon opening, and the emergence of adults. These are often irreversible, specific to particular life stages, and include diapause, an altered physiological state which can be reversed by some synchronizing environmental cue (e.g. photoperiod). However, many successful organisms display none of these mechanisms for maintaining adaptive seasonality. In this paper, we briefly review the mathematical relationship between environmental temperatures and developmental timing and discuss the consequences of viewing these models as *circle maps* from the cycle of yearly oviposition dates and temperatures to oviposition dates for subsequent generations. Of particular interest biologically are life cycles which are timed to complete in exactly 1 year, or univoltine cycles. Univoltinism, associated with reproductive success for many temperate species, is related to stable fixed points of the developmental circle map. Univoltine fixed points are stable and robust in broad temperature bands, but lose stability suddenly to maladaptive cycles at the edges of these bands. Adaptive seasonality may therefore break down with little warning with constantly increasing or decreasing temperature change, as in scenarios for global warming. These ideas are illustrated and explored in the context of Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins) occurring in the marginal thermal habitat of central Idaho's Rocky Mountains. Applications of these techniques have not been widely explored by the applied math community, but are likely to provide great insight into the response of biological systems to climate change.

Keywords: Seasonality; Developmental timing; Circle maps; Nonlinear dynamics; Mountain pine beetle; *Dendroctonus ponderosae*; Climate change; Global warming

1. Introduction

Maintaining an appropriate seasonality is a basic ecological requirement for all organisms. Critical life history events must be keyed to appropriate seasonal cycles in order to avoid lethal temperature or other environmental extremes, coordinate timing of reproductive cycles, avoid predation through simultaneous mass emergence, and a multitude of other requirements for maintaining ecological and biological viability. Seasonality and phenology are essentially synonymous terms that have been used to describe these seasonally predictable events, although seasonality is a more general term referring to both periodic changes in the physical environment and the biological response to these changes. Phenology is specifically used to describe the seasonal progression of a series of biological stages or events. Monitoring seasonality, e.g. seasonal timing of bud-break, has recently gained additional interest as an empirical measure of global climate warming (Menzel and Fabian, 1999).

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Seasonal periodic cycles in photoperiod and temperature are the most obvious stimuli used to maintain an organism's internal clock, and historically the measurement of time has been closely linked to seasonal cycles (Battey, 2000). Warm-blooded (homeothermic) organisms expend a great deal of energy maintaining a constant thermal clock, and for homeotherms time passes at a more or less constant rate. Most organisms (all plants and cold-blooded or poikilothermic animals), however, have metabolisms varying directly with temperature. For these organisms time is relativistic; although other seasonal cues are important, life proceeds faster when things are warm and slower when things are cold. For this reason, monitoring the phenology of plants and poikilotherms (particularly insects) has been used to detect empirical signals of global warming (Hill et al., 1999; Menzel and Fabian, 1999).

Poikilothermic animals like insects face a balancing act when it comes to maintaining appropriate seasonality. On the one hand, it is important to maintain resiliency with respect to the vagaries of weather; e.g. to not be fooled by unusual warm spells in winter or particularly cool summers. On the other hand, it is advantageous to adapt to changing climate to exploit new environments or persist in old ones. In response to these, sometimes opposing, environmental forces, most insects have evolved physiological mechanisms, such as diapause (hibernation, or a state of arrested development that requires specific environmental cues to be terminated) and sensitivity to photoperiod, which serve to re-set and maintain the seasonal clock. Although diapause is an expected norm, many insects, even those living in temperate environments with strong seasonality, apparently lack diapause or any other physiological timing mechanisms. These insects have seasonality that is under direct temperature control (Danks, 1987). Insects with direct temperature control are of particular interest with respect to global change because their phenology should respond immediately, and predictably, to a warming climate.

For insects with direct temperature control of seasonality how can an appropriate seasonality be maintained without some physiological timing mechanism? Adaptive seasonality occurs when (1) individuals emerge at the same time (synchrony), (2) individuals emerge at an appropriate time to utilize resources (timing), and (3) life cycle events are paced to avoid lethal extremes of temperature and environment (seasonality). Gurney et al. (1992) demonstrated that development-free diapause in some life stage is sufficient to cause phase-locking with the seasonal temperature cycle in a theoretical two-stage organism, and expanded on their results in a series of other papers regarding two-stage organisms (Gurney et al., 1994; Grist and Gurney, 1995). Our past work (Bentz et al., 1991; Logan and Bentz, 1999; Powell et al., 2000) has explored adaptive seasonality for the mountain pine beetle, *Dendroctonous ponderose* Hopkins.

The mountain pine beetle is of considerable ecological and economic interest. This insect, which spends its entire developmental life under the bark of host pine trees, is an aggressive tree killer (Samman and Logan, 2000). For this reason, there has been an extensive history of field collection and laboratory rearing for this species. This extensive experience, in our laboratory and others, has failed to indicate diapause or any other physiological timing mechanism other than temperature. Winter collected, or chilled individuals, resume development immediately on warming (Wygant, 1942; Logan and Amman, 1986). Individuals collected from the field in summer can be reared through to adult without chilling (Reid, 1962; Safranyik and Whitney, 1985). No differences in developmental rates are observed between individuals held in cold storage from those reared directly from field collections (J.A.L., unpublished data and personal observations). Considering these observations, and no counter-evidence that we are aware of, it is reasonable to assume that phenology and seasonality are under direct temperature control for the mountain pine beetle.

Although no evidence exists for diapause, the mountain pine beetle exhibits developmental quiescence when temperatures fall below developmental thresholds. Quiescence, in contrast to diapause, occurs when temperatures are so extreme that no development occurs, as when winter temperatures reach such lows that the physiology of the organisms essentially stops for developmental purposes. Unlike diapause, quiescence is reversed as soon as temperatures leave the extreme range; for mountain pine beetle, both quiescence and development occur on almost every winter day in the year as temperatures drop below a thermal threshold at night and then rise above with solar heating during the day. The requirement for synchronous adult emergence for mountain pine beetle is fully described in Logan and Powell (2001), but briefly, a spatio-temporal distribution of oviposition dates must be focused onto a temporally synchronous adult emergence curve to provide the large numbers of attacking beetles required to overcome the substantial defenses of host trees (Raffa and Berryman, 1987). The analytical tools we have developed to analyze phenology and predict seasonality in the mountain pine beetle provide a general framework for any plant or animal with phenology under direct temperature control. Even for organisms with other timing mechanisms (e.g. diapause) or secondary emergence cues (e.g. photoperiod), methods described here can easily be adapted, as we will point out below.

In this article, we explore the quantitative modeling and analysis of direct temperature control and how these models shed light on adaptive seasonality. We first