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Low Seasonal Temperatures Promote
Life Cycle Synchronization

by

Janette Lee Jenkins

A Plan B paper in partial fulfillment
of the requirements for the degree

of

MASTERS OF SCIENCE

in

Industrial Mathematics

Approved:

Abstract

In this paper we discuss how seasonal temperature variation and dormancy can synchronize the development of exothermic organisms. Using a simple aging model it is shown that minimal seasonal temperature variation and periods of dormancy during extreme temperature conditions are sufficient to establish stable, univoltine ovipositional cycles. Dormancy, in fact, promotes synchronous oviposition emergence. The mountain pine beetle, an important insect living in extreme temperature conditions and showing no evidence of diapause, invites direct application of this model. Simulations using mountain pine beetle parameters are used to determine temperature regimes for which stable, ovipositional cycles exist.

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1 Introduction

Synchrony and seasonality are essential to the survival and reproduction of many poikilothermic organisms¹ (Logan and Bentz 1998). Specifically, the Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins, MPB), an important organism in the life cycle of pine forests, must emerge as adults in the appropriate season in order to reproduce. Because their prey, conifers of the genus *Pinus*, have defenses against attack, MPB must attack trees *en masse* in order to successfully lay eggs (Bentz *et. al.*, 1991). This requires that the beetles not only emerge as adults at the right time of the year, but also that the beetles emerge essentially all at once. This becomes very interesting since the eggs may be laid over a 2-3 month period of time, yet adults emerge during a much shorter two week interval (Logan and Bentz, 1999). This indicates that MPB have some mechanism which helps synchronize their emergence.

Many insects use diapause to achieve synchrony and seasonality. Diapause is a state in which growth is suspended and the thermal clock is reset for poikilothermic organisms. This means that the life cycle is synchronized and all the individuals are essentially the same age. However, MPB show no evidence of diapause. Insects with no obvious seasonality timing mechanism, such as diapause, are believed to be under direct temperature control (Danks, 1987). Hence, temperature alone must be responsible for the MPB and other such insects to simultaneously emerge at the appropriate time (Logan and Bentz, 1998).

Logan and Bentz (1999) have developed a model to study direct temperature control as a mechanism for synchrony and seasonality in MPB. The model uses the median adult emergence date as the prediction of when a population of beetles will reach maturity and reproduce. The model includes nonlinear growth curves previously suggested by Logan (1988). If the model is begun on any day of the Julian year, say day 10 for convenience, for generation n and the "beetle" emerges on, say day 10, of the next year, then we say

¹'Poikilothermic' and 'Exothermic' are terms we use here to describe organisms whose body temperature is essentially that of their external environment, *i.e.* 'cold-blooded.'

that generation n began on day 10 and ended on day 10 modulo 1 year, and generation $(n + 1)$ began on day 10. Beginning a "beetle" on every day of the year and running this model over many generations shows that after a few years, successive generations emerge either on a single day every year, a finite set of days, or a cycle (sometimes complex) of days. For a detailed discussion of the model, see Logan and Bentz (1999). The results of the model appear to be robust, suggesting that synchronization may occur for most realistic temperature cycles (Logan and Bentz, 1999).

Each life stage in the MPB has a lethal threshold and a developmental threshold. The lethal threshold is a temperature below which the beetles cannot survive. The developmental threshold is a temperature below which beetles cannot develop, but remain dormant waiting for warmer temperatures (as described by Bentz, *et. al.*, 1991). The lethal threshold, which varies for each developmental life stage, could serve to synchronize emergence by culling those individuals born from eggs laid too late or too early. However, recent evidence indicates that the lethal thresholds are seldom achieved (Bentz and Mullins, 1999) so it is not likely to cause synchronization. The developmental threshold is one of the mechanisms believed to help achieve synchrony and seasonality in insects without diapause (Logan and Bentz 1998). To see how the developmental threshold might help with synchronization, consider two beetles, A and B. Beetle A is laid several days prior to Beetle B. Beetle A finishes the first life stage and molts into the second life stage and continues to grow for say 1 day. Then the temperature drops below the developmental threshold for life stage two but remains above the developmental threshold for life stage one. Beetle A stops developing and becomes dormant. Beetle B meanwhile is still developing in life stage 1. Beetle B finally finishes development for the first life stage and molts into the second life stage. The temperature is below the developmental threshold for life stage two so beetle B immediately becomes dormant. When the temperature rises above the developmental threshold for life stage two, then both beetles resume development, but now they are only one day apart in age. The

developmental threshold for MPB are generally increasing (Powell *et. al.*, 2000) so later life stages enter dormancy sooner than do earlier life stages, which suggests that dormancy may be a strong synchronizing agent

In a previous paper Powell, *et. al.* (2000) described a simplified version of Logan's model with simple seasonal temperature variations and linear developmental rate curves. It was shown that seasonal temperatures swings alone are sufficient to establish seasonality in exothermic organisms. A major *caveat* in that analysis was temperatures were required to remain above developmental thresholds. In this paper, we extend the analysis to the case for which temperatures can drop below developmental thresholds and insects remain dormant for a period of time.

In the next section the mathematical model is presented. In the subsequent section we show that univoltine² solutions exist for an organism with 2 life stages and illustrate the synchronizing effect of dormancy. In the fourth section we present sufficient conditions for existence of a solution for an organism with N life stages. Finally we look at temperature regimes that create voltinism using both linear and nonlinear developmental rate curves and examine voltinism and cyclicity for the mountain pine beetle.

2 The Mathematical Model

The general developmental model for the "age", or fraction of the j th life stage completed, $a_j(t)$, can be written as

$$\frac{da_j}{dt} = R_j(T(t)), \quad a_j(t_{j-1}) = 0. \quad (1)$$

The function $R_j(T)$ is the rate of aging, where t is time and $T(t)$ is the temperature at time t . The developmental age varies between 0 and 1, with t_{j-1} being the time of completion of the $(j-1)$ st life stage and $a_j(t_j) = 1$ (see Figure 1). Formally, one may write the solution

²'Voltinism' refers to the number of generations an organism completes per year. Thus, uni-voltine organisms complete one generations per year, bi-voltine complete two generations per year and so forth.

Figure 1: Univoltine aging for N life stages. The t_j 's on the horizontal axis are the times at which the beetle changes from one life stage to another. Numbers on the vertical axis indicate which life stage is completed thus far. Flat portions of the curve indicate periods during which the beetle is dormant (temperatures below threshold) and not developing.

for t_N , the date of adult emergence, implicitly:

$$\begin{aligned}
 1 &= \int_{t_0}^{t_1} R_1(T(t)) \, dt, \\
 1 &= \int_{t_1}^{t_2} R_2(T(t)) \, dt, \\
 &\vdots \\
 1 &= \int_{t_{j-1}}^{t_j} R_j(T(t)) \, dt, \\
 &\vdots \\
 1 &= \int_{t_{N-1}}^{t_N} R_N(T(t)) \, dt.
 \end{aligned} \tag{2}$$

Analytically, finding a closed-form solution for t_N is not simple (or even possible) in general circumstances, but from a computational perspective one simply integrates to 1 repeatedly, saving the final result. The complications of nonlinear rate curves and non-constant temperature series would probably necessitate computational approaches in any event. For any given temperature regime, t_N will depend on t_0 — the time of the year during which the egg was laid and consequently we may think of t_N as a map of t_0 . Since every ovipositional date, t_0 , generates at most one emergence date and time, t_N , we may write t_N as a function

$$t_N = G(t_0). \quad (3)$$

Temperatures, of course, are rarely constant through the year. Taking t to be measured in years, with $t = 0$ at the average yearly minimum temperature (say January 30), a simple mathematical model for seasonal variation of temperature (Taylor, 1981) is

$$T(t) = T_0 - T_1 \cos(2\pi t). \quad (4)$$

In this equation T_0 is the yearly average temperature and T_1 is the size of the seasonal contribution to yearly temperature swings; that is, $2T_1$ is the temperature difference between the coldest and hottest parts of the year. The behavior of yearly temperature is *much* more complicated than this, but as has been shown by Powell, *et. al.* (2000), this minimal seasonality is enough to establish voltinism. Conversely, the additional terms needed to improve the accuracy of $T(t)$ are not, within limits, sufficient to destroy voltinism.

The sequence of equations, (2), resulting in t_N , can be thought of as a map from the interval $[0,1]$ into itself. Ovipositional dates cycle from 0 to 1 and then repeat, so solutions for t_N are interpreted modulo 1. This creates the possibility for fixed points and strong seasonality; if $t_N = 1 + t_0$ then t_0 is an equilibrium solution for oviposition corresponding to a univoltine cycle. Similarly, if

$$t_N = m + t_0$$

then t_0 is an equilibrium solution for an $\frac{1}{m}$ -voltine cycle.

Suppose $R_j(T)$ is the simplest possible linear temperature-dependent rate of development.

Thus,

$$R_j(T) = \max[0, r_j(T(t) - \theta_j)]. \quad (5)$$

where

$$r_j(T(t) - \theta_j) = r_j[T_0 - \theta_j - T_1 \cos(2\pi t)] \quad (6)$$

In (6), the parameters r_j and θ_j are life stage specific constants; r_j is the linear rate of development for temperatures above threshold and θ_j is the developmental threshold temperature for life stage j . In regions where MPB live the temperature is quite cold during much of the year, often below the developmental threshold, θ_j (see Figure 2). Analytically, it is cumbersome to carry the $\max[0, r_j(T - \theta_j)]$, so instead we elect to subtract out periods of time during which $R_j < 0$ in (2), that is, we express aging for life stage j as

$$1 = \int_{t_{j-1}}^{\xi_{1j}} R_j(T(t))dt + \int_{\xi_{2j}}^{t_j} R_j(T(t))dt = \int_{t_{j-1}}^{t_j} R_j(T(t))dt - \int_{\xi_{1j}}^{\xi_{2j}} R_j(T(t))dt. \quad (7)$$

Here t_{j-1} is the time at which the insect completes life stage $j - 1$ and begins life stage j . Similarly, t_j is the time at which the insect completes life stage j and begins life stage $j + 1$. The beginning of a dormancy period in life stage j is ξ_{1j} and the end of the same dormancy period is ξ_{2j} . Equation (7) can be rewritten as

$$1 = f_j(t_{j-1}, t_j) - \int_{\xi_{1j}}^{\xi_{2j}} R_j(T(t))dt, \quad (8)$$

with

$$f_j(t_{j-1}, t_j) \stackrel{\text{def}}{=} [(T_0 - \theta_j)(t_j - t_{j-1}) - \frac{T_1}{2\pi}(\sin(2\pi t_j) - \sin(2\pi t_{j-1}))] \quad (9)$$

and $\int_{\xi_{1j}}^{\xi_{2j}} R_j(T(t))dt$ expanded as

$$r_j \left[(T_0 - \theta_j)(\xi_{2j} - \xi_{1j}) - \frac{T_1}{2\pi}(\sin(2\pi \xi_{2j}) - \sin(2\pi \xi_{1j})) \right]. \quad (10)$$

Figure 2: The temperature curve, $T(t) = T_0 - T_1 \cos(2\pi t)$, used in the model. T_0 is the mean annual temperature, T_1 is the size of the seasonal fluctuations, and θ_j is the developmental threshold for life stage j . For times between ξ_{1j} and ξ_{2j} the temperature is below the developmental threshold, that is, $(T_0 - T_1) < \theta_j$.

Suppose temperature is below the developmental threshold for life stage j (as in Figure 2).

To find the points at which the temperature equals the threshold, set

$$\theta_j = T_0 - T_1 \cos(2\pi \alpha_j).$$

Solving for α_j gives

$$\alpha_j = \frac{1}{2\pi} \cos^{-1} \left[\frac{T_0 - \theta_j}{T_1} \right].$$

Due to the periodic temperature curve, critical points occur at α_j , $1 \pm \alpha_j$, $2 \pm \alpha_j$, ..., depending at what time of the year development begins.

To see why we distinguish between α_j and ξ_j consider Figure 3. For a beetle developing in life stage j , if the temperature goes below θ_j , then the beetle stops developing until the temperature rises above θ_j again. In this case zero aging begins and ends at two successive

α_j s, e.g., α_j & $1 - \alpha_j$ or $1 - \alpha_j$ & $1 + \alpha_j$ or $1 + \alpha_j$ & $2 - \alpha_j$ (see Figure 3-A), a situation referred to as a “stop”. If the thresholds are increasing between life stages $j - 1$ and j , then the beetles could finish development of life stage $j - 1$ and move into life stage j . However, if that temperature at t_{j-1} is below θ_j , then the beetles will become dormant at the beginning of life stage j and remain so until the temperature rises above θ_j at which time development for that life stage begins, a situation we refer to as a “speed bump”. In this case the zero aging period is begun at t_{j-1} and ended at one of the α_j s. (see Figure 3-B). For both situations, we call the beginning and end of dormancy ξ_{1j} and ξ_{2j} , respectively.

Figure 3: This figure shows two ways to incorporate dormancy into a temperature series. **A** (stop) shows the case where both endpoints of dormancy, τ_1 and τ_2 , are functions of α_j . **B** (speed bump) shows the case where the first endpoint, τ_1 , is the beginning of the life stage and the second endpoint, τ_2 , is a function of α_j .

We have defined $t_N = G(t_0)$. We also know that an m -voltine life cycle exists if $t_N = m + t_0$. Hence if $G(t_0) = m + t_0$, then we must have an m -voltine solution for t_0 and t_N . Here we are interested in univoltine life cycle — $m = 1$. Hence we look for places where the curves

$t_N = G(t_0)$ and $t_N = 1 + t_0$ cross (see Figure 4). It was shown by Powell *et. al.* (2000) that

Figure 4: Crossing of $G(0)$ and $t_N = 1 + t_0$. The dotted curve is $G(0)$ without any dormancy and the solid curve is $G(0)$ with dormancy. When dormancy is added, then $G(0)$ and t_N are more likely to cross.

if the temperature never falls below the developmental threshold then a univoltine solution exists. In Figure 4 the dashed line represents $t_N = 1 + t_0$, the dotted line is $G(t_0)$ when the temperature always remains above the developmental threshold, and the solid line is $G(t_0)$ when dormancy is added to the model.

If $G(0)$ is only slightly larger than 1, then dormancy increases the likelihood of a crossing because of the regions with zero slope. Such flat regions result from t_0 beginning when temperature is below θ_1 (speed bump), when the egg is laid, the egg immediately enters dormancy and no development occurs until the temperature rises above θ_1 . Two eggs laid at different times but both while $T(t) < \theta_1$ will be the same age when they leave dormancy

and will therefore have the same emergence date, t_N . Discontinuities in $G(t_0)$ occur when dormancy causes two insects that are similar in age to diverge, having very different emergence dates. To see how this occurs, consider two beetles developing in life stage j only one day apart in age. The first beetle ends life stage j and molts into life stage $j + 1$. Then temperature falls below the developmental threshold for life stage j , causing the second beetle to become dormant. The first beetle continues to develop, causing the two beetles to have very different emergence dates, t_N . Overall, then, there are two competing effects: regions of $G(t_0)$ with zero slope serve to increase the likelihood of $t_N = G(t_0)$ and $t_N = 1 + t_0$ crossing, while discontinuities in $G(t_0)$ reduce the likelihood of crossing. Next we will determine which effect dominates in an organism with only two life stages.

3 Two Life Stage Example

Consider an insect with two life stages, *e.g.*, an egg and an adult, and suppose life stage 1 begins during the coldest part of the year. In addition, let life stage 1 have a developmental threshold above the minimum yearly temperature and let life stage 2 have a developmental threshold below the yearly minimum temperature, thus the insect could experience dormancy in life stage 1 but not in life stage 2 (See Figure 5).

Assume an insect egg is laid at $t = 0$. The temperature is below the developmental threshold so the insect is dormant. The insect remains dormant until $t = \alpha_1$ and all eggs laid between $t = 0$ and $t = \alpha_1$ would have the same emergence date, t_2 . This causes the function $G(t_0)$ to be flat between 0 and α_1 . If $G(t_0)$ in this region crosses $t_2 = 1 + t_0$, then we could have a univoltine solution.

The development equations for this case are

$$1 = r_1 \left[(T_0 - \theta_1)(t_1 - \alpha_1) - \frac{T_1}{2\pi} (\sin(2\pi t_1) - \sin(2\pi \alpha_1)) \right], \quad (11)$$

$$1 = r_2 \left[(T_0 - \theta_2)(t_2 - t_1) - \frac{T_1}{2\pi} (\sin(2\pi t_2) - \sin(2\pi t_1)) \right]. \quad (12)$$

Figure 5: Temperature Curve for univoltine life cycle for 2 Life Stage Insect which experiences dormancy in life stage 1 but not in life stage 2.

We want to show that the curves $t_2 = G(t_0)$ and $t_2 = 1 + t_0$ cross. Since we have a flat area in $G(t_0)$ that we know ends at $t = \alpha_1$, we look for a crossing between 0 and α_1 . First we find an upper bound for $G(t_0)$ between t_0 values of 0 and α_1 that crosses $t_2 = 1 + t_0$ at $t_0 = \alpha_1$, and then we show that $G(t_0) > 1$ but less than the upper bound.

If we sum equations (11) and (12), weighted by $\frac{1}{r_1}$ and $\frac{1}{r_2}$, respectively we get

$$\frac{1}{r_1} + \frac{1}{r_2} = (T_0 - \theta_1)(-\alpha_1) + (T_0 - \theta_2)t_2 + (\theta_2 - \theta_1)t_1 + \frac{T_1}{2\pi} \sin(2\pi\alpha_1) - \frac{T_1}{2\pi} \sin(2\pi t_2). \quad (13)$$

We know that $\alpha_1 < t_1$ (since the first life stage cannot complete before development begins), and the second order Taylor expansion gives $1 - 4\pi^2(t_2 - \frac{1}{4})^2$, a parabola which is less than $\sin(2\pi t_2)$. We substitute these values into (13) to get

$$\frac{1}{r_1} + \frac{1}{r_2} \leq (T_0 - \theta_2)(t_2 - \alpha_1) + \frac{T_1}{2\pi} \sin(2\pi\alpha_1) - \frac{T_1}{2\pi} (1 - 4\pi^2(t_2 - \frac{1}{4})^2) \quad (14)$$

Equation (14) is a quadratic inequality, and solving for t_2 generates upper and lower bounds as seen in Figure 6. Using equation (13), we choose a value for t_1 that is less than 1 (otherwise the solution is clearly not univoltine) and solve for t_2 . We find that there exists a value for $t_2 > t_1$ and less than the upper bound for t_2 (the dotted line) as seen in the

Figure 6: The plot on the left shows the upper and lower bounds for t_2 for a two life stage insect. The upper bound crosses the angled line $t_2 = 1 + t_0$ at $t_0 = \alpha_1$. The plot on the right shows where an actual life cycle could exist (the dashed line). Where this dashed line crosses $t_2 = 1 + t_0$ gives values for t_0 and t_2 where a univoltine life cycle will exist for the parameter values used. The horizontal axis is t_0 and the vertical axis is t_2 .

right plot of Figure 6. Since $t_2 > t_1$ the solution is consistent, and consequently we have shown that a univoltine solution exists. A solution is dynamically stable if $G'(t_0) < 1$. In this case, the solution is super stable because $G'(t_0) = 0$. Thus, if we choose a value of t_0 nearby the one used in the example, then a solution will still exist. In addition, the solution is structurally stable since the curves cross transversely, thus the parameter values can be changed within limits without destroying the crossing of the two curves. Structural stability also implies that any “nearby” model in which this model is imbedded will also have a stable solution. This suggests that the results for two life stages are generic and can be generalized to N -stage organisms. This also implies that the same organism should enjoy strong seasonality for a range of temperature regimes including environments in which temperatures are not perfectly periodic. The simulation results of Logan and Bentz (1999), using realistic temperature series, indicates that this is the case. The hypothesis that multi-stage organisms can experience direct temperature control of seasonality will be further

examined in the next section.

4 N Life Stages

For N life stages, we need only show that a solution exists, that is, we must show that the curves $t_N = G(t_0)$ and $t_N = 1 + t_0$ cross. To do so, we show that t_N has an upper bound for $t_0 < \alpha_1$ and show that $t_N = G(t_0)$ is between 1 and the upper bound when $t_0 < \alpha_1$, forcing a crossing. It is possible that crossings exist for other values of t_0 (In fact, our numerical results indicate that this is, indeed, the case), but we will show that there exists at least one t_0 that generates a univoltine life cycle. By restricting attention to the interval prior to $t = \alpha_1$ (the beginning of development) we avoid the discontinuities discussed previously.

Traditionally we measure a life cycle from the egg to the egg in the next generation. We could just as easily define generation time from the completion of any life stage to the completion of that life stage in the next generation, *e.g.*, first larval instar to first larval instar, or pupae to pupae. Here we choose to define generation time by the life stage with the *highest* developmental threshold. If the temperature is at its minimum during the life stage with the maximum developmental threshold, then organisms in the other life stages will not experience dormancy in a univoltine life cycle, simplifying the problem. In addition, the life stage with the highest developmental threshold has the longest period of dormancy maximizing the amount of $G(t_0)$ with zero slope. For MPB the pupal stage has the highest developmental threshold, so we reorganize the life stages such that

$$\phi_1 = \theta_6, \phi_2 = \theta_7, \phi_3 = \theta_1, \dots, \phi_7 = \theta_5$$

and

$$\rho_1 = r_6, \rho_2 = r_7, \rho_3 = r_1, \dots, \rho_7 = r_5.$$

Now ϕ_i are the newly ordered developmental thresholds and ρ_i are the reordered linear developmental rates, with i being ordered beginning with the highest developmental threshold

and continuing through the other $N - 1$ life stages in sequential order. In addition, we reset the clock so that time begins at the point where temperature passes below the first (and highest) developmental threshold. In Figure 7, the plot on the left shows time and temperature prior to reorganization. The figure on the right shows a new time scale with $\tau = 0$

Figure 7: This figure shows how we shift the time scale so that time is zero is occurs when dormancy begins for the life stage with the highest developmental threshold.

at the former $t = -\alpha_1$, and $T(t) = T_0 - T_1 \cos(2\pi(\tau - \alpha_1))$ with $\tau = t + \alpha_1$. Hence τ_0 is the time the insect begins the stage with the highest developmental threshold and τ_N is the time the insect finishes the life stage just prior to the one with the highest developmental threshold and begins a new generation. In MPB, τ_0 is inception of pupal life stage and τ_7 is the time of completion of the fourth larval instar.

The aging equations (2) become

$$1 = \int_{\tau_{j-1}}^{\tau_j} \max[0, \rho_j(T - \phi_j)] d\tau. \quad (15)$$

Suppose $\tau_0 \in [0, 2\alpha_1]$. No development occurs until $\tau > 2\alpha_1$, and consequently aging in the pupal stage satisfies

$$\frac{1}{\rho_1} = \int_{2\alpha_1}^{\tau_1} [T_0 - T_1 \cos(2\pi(\tau - \alpha_1)) - \phi_1] d\tau \quad (16)$$

$$= (T_0 - \phi_1)(\tau_1 - 2\alpha_1) - \frac{T_1}{2\pi} (\sin(2\pi(\tau_j - \alpha_1)) - \sin(2\pi(\tau_{j-1} - \alpha_1))). \quad (17)$$

Now define α_2 to be the time at which temperatures cross the next lower threshold. If $t_N = \tau_N - \alpha_1 \leq 1 - \alpha_2$, then $\tau_N \leq 1 + \alpha_1 - \alpha_2$, and for such τ_N no other development

thresholds are crossed during a univoltine life cycle (thus avoiding discontinuities). The remaining equations for development can then be written

$$\frac{1}{\rho_j} = (T_0 - \phi_j)(\tau_j - \tau_{j-1}) - \frac{T_1}{2\pi}(\sin(2\pi(\tau_1 - \alpha_1)) - \sin(2\pi(\tau_{j-1} - \alpha_1))). \quad (18)$$

Summing (17) and (18), we get

$$\begin{aligned} \sum_{j=1}^N \frac{1}{\rho_j} &= T_0(\tau_N - 2\alpha_1) - \tau_N \phi_N + 2\alpha_1 \phi_1 \\ &+ \tau_1(\phi_2 - \phi_1) + \tau_2(\phi_3 - \phi_2) + \dots + \tau_{N-1}(\phi_N - \phi_{N-1}) \\ &+ \frac{T_1}{2\pi}(\sin(2\pi\alpha_1) - \sin(2\pi(\tau_N - \alpha_1))). \end{aligned} \quad (19)$$

For future reference

$$A \stackrel{\text{def}}{=} \tau_1(\phi_2 - \phi_1) + \tau_2(\phi_3 - \phi_2) + \dots + \tau_{N-1}(\phi_N - \phi_{N-1}).$$

We are interested in $\tau \in [1, 1 + \alpha_1 - \alpha_2)$, that is, times of completion satisfying $G(\tau_0) > 1$ but avoiding discontinuities, so we write

$$\tau_N = 1 + \alpha_1 - \delta, \quad \delta \in (0, \alpha_2).$$

Now we estimate

$$\sin(2\pi(\tau_N - \alpha_1)) = \sin(2\pi(1 - \delta)) \geq \sin(2\pi) - 2\pi\delta \cos(2\pi) = -2\pi\delta.$$

using Taylor's Theorem. It follows that

$$-\frac{T_1}{2\pi} \sin(2\pi(\tau_N - \alpha_1)) \leq \frac{T_1}{2\pi} 2\pi\delta = T_1\delta = T_1(1 + \alpha_1 - \tau_N).$$

Therefore,

$$\begin{aligned} \sum_1^N \frac{1}{\rho_j} &\leq (T_0 - \phi_N)\tau_N - 2\alpha_1 T_0 + A + \frac{T_1}{2\pi} \sin(2\pi\alpha_1) + T_1(1 + \alpha_1 - \tau_N) \\ &= \tau_N(T_0 - \phi_N - T_1) + A + T_1(1 + \alpha_1) - 2\alpha_1 T_0 + \frac{T_1}{2\pi} \sin(2\pi\alpha_1). \end{aligned} \quad (20)$$

In general, $T_0 - \phi_N - T_1 < 0$, so if we solve (20) for τ_N we get an upper bound

$$\tau_N \leq \frac{A + T_1(1 + \alpha_1) - 2\alpha_1 T_0 + \frac{T_1}{2\pi} \sin(2\pi\alpha_1) - \sum_{j=1}^N \frac{1}{\rho_j}}{T_1 + \phi_N - T_0}. \quad (21)$$

Lastly, we must find an overestimate for A . If $\phi_j - \phi_{j-1} < 0$ then $\phi_j - \phi_{j-1} \stackrel{\text{def}}{=} D_j$ and if $\phi_j - \phi_{j-1} > 0$ then $\phi_j - \phi_{j-1} \stackrel{\text{def}}{=} U_j$. Because we do not know how many $(\phi_j - \phi_{j-1})$'s will be positive and how many will be negative, we have to bound both $\sum_j D_j$ and $\sum_j U_j$ by known quantities that are independent of the individual D_j 's and the U_j 's.

$D_j < 0$, therefore $\sum_j D_j < 0$. In addition, $\sum_j U_j \leq (\phi_1 - \phi_{\min})$ which is the largest developmental threshold minus the smallest developmental threshold. This is the maximum for $\sum_j U_j$. Now, $\tau_N \geq (\tau_j)_{\max}$ so $\sum_j \tau_j U_j \leq \tau_N (\phi_1 - \phi_{\min})$. Therefore,

$$A < (\phi_1 - \phi_{\min})\tau_N. \quad (22)$$

Substituting (22) for A in (21) and solving for τ_N , we get

$$\tau_N \leq \frac{-2\alpha_1 T_0 + \frac{1}{2\pi} \sqrt{T_1^2 - (T_0 - \phi_1)^2} - \sum_{j=1}^N \frac{1}{\rho_j} + T_1(1 + \alpha_1)}{T_1 - \phi_1 - T_0 + \phi_N + \phi_{\min}}. \quad (23)$$

Now,

$$\cos(2\pi\alpha_1) = \cos\left(\cos^{-1}\left(\frac{T_0 - \phi_1}{T_1}\right)\right) = \left(\frac{T_0 - \phi_1}{T_1}\right).$$

Solving for the third side of the triangle using the Pythagorean Theorem and taking the sine using the triangle replaces $\frac{T_1}{2\pi} \sin(2\pi\alpha_1)$ with $\frac{1}{2\pi} \sqrt{T_1^2 - (T_0 - \phi_1)^2}$ in (23).

To see how the bound behaves, consider $T_1 = T_0 - \phi_1$. This is the minimum value for T_1 , otherwise temperature would never be above the developmental threshold for life stage 1 and no growth could occur. At $T_1 = T_0 - \phi_1$, $\alpha_1 = 0$ so the bound becomes

$$\tau_N \leq \frac{\sum_{j=1}^N \frac{1}{\rho_j} - (T_0 - \phi_1)}{2\phi_1 - \phi_N - \phi_{\min}} \quad (24)$$

which could be positive, though likely small, or negative depending on parameters. As $T_1 \rightarrow \infty$, $\alpha_1 \rightarrow \frac{1}{4}$, and

$$\tau_N \leq 1 + \frac{1}{2\pi} + \alpha_1. \quad (25)$$

Because we want a univoltine solution, we need a bound on τ_N that is larger than 1. As T_1 increase this condition is more easily satisfied suggesting that large seasonal temperature swings help to promote univoltine life cycles.

Figure 8: This figure shows why $\tau_N < 1 + 2\alpha_1$ for a univoltine life cycle to exist.

Because development cannot begin before $2\alpha_1$, then to be certain that a univoltine cycle exist, $\tau_N \leq 1 + 2\alpha_1$ (see figure 8). Setting the right hand side of (23) $\leq 1 + 2\alpha_1$ we find that

$$\frac{T_1 + \frac{1}{2\pi} \sqrt{T_1^2 - (T_0 - \phi_1)^2} - \sum_{j=1}^N \frac{1}{\rho_j} + 2\alpha_1(\phi_1 - \phi_{min} - \phi_N - \frac{T_1}{2})}{T_1 + \phi_N - T_0 - \phi_1 + \phi_{min}} \leq 1 \quad (26)$$

which for reasonable values of T_0 and T_1 is easily satisfied.

We have shown that it is possible for univoltine solutions to exist. We now use MPB parameters to find yearly temperature regimes that support the theory developed previously.

5 Application to MPB

MPB shows no evidence of diapause, yet maintains synchrony and appropriate seasonality. Figure 9 shows the actual developmental rate curves for MPB (Powell *et. al.*, 2000) estimated

previously (Logan and amman 1986; Bentz *et. al.* 1991; Logan and Bentz 1999) with the linearizations approximated from these curves (shown as the dotted lines in Figure 9) (Powell *et. al.* 2000). Determining true development thresholds for this insect in laboratory experiments has proven difficult. Larvae feed and develop within the cryptic habitat of tree phloem. It is extremely difficult to maintain an appropriate environment for the length of time required to monitor development at low temperatures. Due to these problems, our current best estimate of low temperature developmental thresholds for this insect are those derived from the nonlinear rate curves. The parameter values for the linear model are found in Table 1.

Developmental Stage	Developmental Threshold	Linear Rate
Egg	$\theta_1 = 7.5394$	$r_1 = 4.1975$
First Larval Instar	$\theta_2 = 8.6358$	$r_2 = 10.6945$
Second Larval Instar	$\theta_3 = 9.6322$	$r_3 = 10.4390$
Third Larval Instar	$\theta_4 = 8.0342$	$r_4 = 3.4675$
Fourth Larval Instar	$\theta_5 = 10.9543$	$r_5 = 3.6500$
Pupae	$\theta_6 = 11.7555$	$r_6 = 6.2780$
Ovipositional Adult	$\theta_7 = 1.7929$	$r_7 = 1.2775$

Table 1: Parameters for linearized rates of development for mountain pine beetle, including developmental thresholds, θ_j . Temperatures are measured in degrees centigrade, while developmental rates, r_j , have units of inverse degrees per year (Powell *et. al.*, 2000)

By iterating the ovipositional map for many generations we are able to determine which seasonal cycles, if any, are attracting. For the case with daily temperature fluctuations the temperatures will be modeled using the truncated Fourier series

$$T(t) = T_0 - T_1 \cos(2\pi t) - T_{365} \cos(2\pi t/365).$$

We set $T_{365} = 0$ for simulations which have only seasonal temperature fluctuations. Equations (2) were integrated using the trapezoid rule in MATLAB with arbitrarily chosen initial conditions, t_0 , for at least 100 generations of developmental time, and the sequence of ovipositional dates were examined for seasonality. The emergence date for each year is recorded.

Figure 9: Nonlinear rate curves for MPB (solid) and linear approximations (dashed) with developmental thresholds and linear rates of development. From left to right, top to bottom the curves represent rates of development for (a) eggs, (b) first larval instar, (c) second larval instar, (d) third larval instar, (e) fourth larval instar, (f) pupae and (g) ovipositional adults. Open circles represent developmental data, while 'x' represent data selected to parametrize a purely linear representation of the developmental rate.

Seasonality is achieved if after a “few” years, the emergence date remains the same for all following years. In addition, for each choice of T_0, T_1 the number of generations per year at the end of the simulation were recorded. A contour plot of the seasonalities for seasonal fluctuations only is presented in Figure 10. The white areas are regions of stable voltinism. The black and white marbled areas are regions of fractional or asynchronous voltinism. Such voltinism occurs if one year does not contain an integer number of generations, *e.g.*, $m = 3.4$. Though MPB generally live in temperate environments, they require an adequate amount of thermal energy for development. Figure 10 illustrates this; if the mean annual temperature (T_0) is high, then only small seasonal fluctuations are required to achieve univoltine life cycles. However, if the mean annual temperature is low, then large seasonal temperature fluctuations are required to acquire enough thermal energy for development through all seven life stages.

Figure 11 depicts the regions of voltinism when daily fluctuations are included. In this case $T_0 = 3$ degrees Centigrade. Daily fluctuations reduce the size of seasonal fluctuations required for successful synchrony by approximately one degree Centigrade. This occurs because beetles acquire more energy on some days due to daily temperature fluctuations. The lower bound for T_1 is decreased, generating a larger set of temperatures which create stable univoltine life cycles, increasing the success of MPB. In Figure 10 the bands of stable voltinism are separated by regions of fractional voltinism. It has been hypothesized (Logan and Bentz 1999) that an increase in mean annual temperature from inside to outside the regions of voltinism destabilizes life cycles before the temperature reaches another region of stable integer voltinism. This would lead to unsuccessful reproduction, limiting MPB distribution.

For organisms with many life stages, the development may be approximated by linear rate curves (Powell, *et. al.*, 2000), however, Logan *et. al.* (1976) (and many others before) provide evidence that arthropods have nonlinear developmental rate curves. Table 2 shows the

Figure 10: This figure shows the combinations of mean annual temperatures, T_0 , and seasonal fluctuations, T_1 , for which the model using the linear development growth rate curves predicts $\frac{1}{m}$ -voltine life cycles. The white areas are regions of stable voltinism. The black and white marbled areas are regions of asynchronous fractional voltinism.

Figure 11: This figure shows the combinations of seasonal temperature fluctuations, T_1 , and daily temperature fluctuations, T_{365} , when the mean annual temperature, $T_0 = 3$, predicts $\frac{1}{m}$ -voltine life cycles using the linear development rate curves. The white areas are regions of stable voltinism. The black and white marbled areaa are regions of asynchronous fractional voltinism.

functional forms for developmental rate curves depicted in Figure 9, followed by parameter values for the nonlinear rate curves in Table 3.

Developmental Stage	Temperature Inputs	Functional Forms for $T > 0$
Egg	$T = T(t)$	$p_1 \left[\frac{1}{1+p_2 \exp(-p_3(T-5))} - \exp\left(\frac{-p_4+T+5}{p_5}\right) \right]$
First Larval Instar	$T = T(t)$	$p_1 \left[\frac{1}{1+p_2 \exp\{-p_3(T-5)\}} - \exp\left(\frac{-p_4+T+5}{p_5}\right) \right]$
Second Larval Instar	$T = T(t)$	$p_1 \left[\frac{1}{1+p_2 \exp\{-p_3(T-10)\}} - \exp\left(\frac{-p_4+T+5}{p_5}\right) \right]$
Third Larval Instar	$T = T(t)$	$p_1 \left[\frac{1}{1+\left(\frac{p_4}{T-p_5}\right)^2} - \exp\left(\frac{T-p_2-p_5}{p_3}\right) \right]$
Fourth Larval Instar	$T = T(t)$	$p_2(T - p_1)$
Pupae	$T = T(t)$	$p_2(T - p_1)$
Ovipositional Adult	$T = T(t)$	$2.54p_1 \left[\exp(p_2(T - p_5)^{p_3}) - \exp\left(\frac{p_5-T}{p_4}\right) \right]$

Table 2: Functional forms for nonlinear development for mountain pine beetles. The functional form for each of the life stages is used if the development is positive, otherwise the rate is set to zero. The third larval stage and the ovipositional adult stage have the additional requirement that the temperature must be above the developmental threshold, p_5 , or else rates are set to zero for these life stages.

Figure 12 shows that the nonlinear developmental rate functions decrease the size of temperature regions for which voltinism is achieved as compared with the linear curves. It does not remove the regions of asynchronous fractional voltinims separating regions of stable voltinism. Contrary to the model outcome using linear developmental rate curves, when daily fluctuations are added to the model with nonlinear developmental rate curves, the regions of stable voltinism are decreased (see Figure 13). This is due to the modal nonlinear developmental rate curves (see Figure 9). At high temperatures the linear model overestimates the amount of development occurring in the first four life stages. The linear rate curves increase as temperature increases, whereas the nonlinear rate curves have a mode

Developmental Stage	p_1	p_2	p_3	p_4	p_5
Egg	0.3148	19.9353	0.2034	29.6029	4.8851
First Larval Instar	0.6887	57.2790	0.3004	25.2244	4.5963
Second Larval Instar	0.3562	18.0117	0.4788	19.3602	3.4696
Third Larval Instar	0.1909	19.7005	0.1542	8.7683	7.9046
Fourth Larval Instar	10.9543	0.0100			
Pupae	11.7555	0.0172			
Ovipositional Adult	0.1690	0.0194	1.5400	0.8000	2.0000

Table 3: Parameters for nonlinear rates of development for mountain pine beetle.

in the 20's and then decrease as temperature continues to rise. In the linear model, the beetle increases in age at these high temperatures while in the nonlinear model, the beetle does not develop as much at those temperatures. For this reason, the linear model accelerates aging and finds more regions of T_0, T_1 in which there is enough thermal energy for life cycle completion.

6 Conclusions

Seasonal synchrony and Seasonality are vital to the survival and reproduction of MPB. We see that temperature variations alone are enough to create conditions for univoltine life cycles, promoting synchrony and seasonality. Furthermore, periods in the life cycle during which an insect is dormant enhance univoltinism. As seen in the simulations, bivoltine (and multivoltine) life cycles are also possible when enough thermal energy exists in the system, *i.e.*, high mean annual temperature with large seasonal fluctuations. Exothermic organisms with one high developmental threshold cause these cyclic solutions to be extremely stable because parameters can be varied generously while maintaining the crossing of the curves $t_N = 1 + t_0$ and $t_N = G(t_0)$ in the flat region of $G(t_0)$. In fact, observed field temperatures do indeed create stable univoltine life cycles (Logan and Bentz, 1999).

In this paper we have shown that univoltine solutions exist for reasonable temperature regimes. There are, however, many possible fixed points for the system not all of which are

Figure 12: This figure shows the combinations of T_0 and T_1 for which the model using the nonlinear development rate curves predicts $\frac{1}{m}$ -voltine life cycles. The white areas are regions of stable voltinism. The black and white marbled areas are regions of asynchronous fractional voltinism.

Figure 13: This figure shows the combinations of seasonal temperature fluctuations, T_1 , and daily temperature fluctuations, T_{365} , when the mean annual temperature $T_0 = 3$ degrees that generate $\frac{1}{m}$ -voltine life cycles using the nonlinear development rate curves. The white areas are regions of stable voltinism. The black and white marbled area are regions of asynchronous fractional voltinism.

univoltine. As seen in simulations, suitable conditions for univoltinism are fairly restricted. Some modification in the temperature, two degrees in either mean or seasonal temperatures (such as occurs from global warming and is well within limits predicted) may alter or destroy the voltinism that makes MPB successful. Since MPB are an important participant in the life of a Pine forest, the alteration or loss of life cycles for MPB could have far reaching effects. Though MPB are generally associated with temperate regions, they are expanding into warmer climates. As they do so, the asynchronous voltinism is observed due to a prolonged emergence period. This supports the hypothesis that thermal habitat is one factor limiting the southern distribution of MPB (Logan and Bentz, 1999).

If global warming continues to cause the mean annual temperature to increase, the climate in their current habitat may warm, thrusting MPB into asynchronous fractional voltinism in those regions. Survival may force MPB to migrate into new regions that would promote integer voltine life cycles. This model could be used to determine what future habitats, based on temperature, the MPB may inhabit. Because pine forest depend on natural predators and fire to incite new growth, this model may be to study how the change in synchrony and seasonality may affect the life cycles of pine trees and other organisms in MPB habitat.

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