

Seasonal Temperature Alone Can Synchronize Life Cycles

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In this paper we discuss the effects of yearly temperature variation on the development and seasonal occurrence of poikilothermic organisms with multiple life stages. The study of voltinism in the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), an important forest insect living in extreme temperature environments and exhibiting no diapause, provides a motivational example. Using a minimal model for the rates of aging it is shown that seasonal temperature variation and minimal stage-specific differences in rates of aging are sufficient to create stable uni- and multi-voltine oviposition cycles. In fact, these cycles are attracting and therefore provide an exogenous mechanism for synchronizing whole populations of organisms. Structural stability arguments are used to extend the results to more general life systems.

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1. INTRODUCTION

Maintaining an appropriate seasonality is among the most basic requisites for poikilothermic[†] organisms living in temperate environments. Critical life-history events must be appropriately timed with seasonal resource abundance. Successful adaptation to times of seasonal stress (e.g., winter, dry season) also require timing of a particular life stage to correspond with seasonal environmental cues. In addition to timing, an adaptive seasonality often requires synchronous occurrence of specific life stages. Adult mayflies, for example, must simultaneously occur over

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[†]‘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’.

their ephemeral reproductive life span in order to find mates. In fact, the requirement for synchrony is widespread throughout the Class Insecta, with basic fitness attributes such as successfully overcoming host defenses and predator avoidance requiring simultaneous occurrence of large numbers of individuals. The two basic components of seasonality are, therefore, timing and synchrony. Temperature is the most basic controller of seasonality in poikilothermic organisms (Zaslavski, 1988) and a large body of literature exists relating the effects of temperature to developmental rates and phenology. These seasonal models typically require some starting point or 'biofix' where all members of the population are approximately the same age. For insects this biofix has often been the breaking or termination of diapause.

Diapause is a physiological hibernal state that functions, among other things, to reset the thermal clock for cold-blooded organisms. Diapause is therefore basic to maintaining an appropriate seasonality and is widely expressed in terrestrial insects. It has been argued, in fact, that diapause is an early evolutionary adaptation of insects due to its almost universal expression (Zaslavski, 1988). Some insects, for example most aquatic species, exhibit no diapause. There are also some terrestrial species in which diapause is lacking. Maintaining seasonality without some obvious mechanism to reset the thermal clock has been termed direct control of seasonality (Danks, 1987). Since maintaining an adaptive seasonality is no less important for insects under direct temperature control than those with diapause, an interesting question is: how can adaptive seasonality be maintained without some physiological mechanism such as diapause?

The goal of this paper is to prove that seasonal temperature swings *alone* are sufficient to establish seasonality in exothermic organisms, without diapause or other physiological mechanisms to reset the thermal clock. Our work shows that within realistic parameter regimes uni-, semi- and multi-voltine[‡] cycles are possible and indeed structurally stable. In the first section we will present the basic models for aging and life stage transition as well as environmental temperature. In the second section we will illustrate the techniques to be used in an hypothetical two-stage organism. In the third section we will establish sufficient conditions for the existence of seasonality in N -stage organisms and discuss the structural stability[§] of the voltine cycles. These results will be applied to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, hitherto abbreviated MPB) in the fourth section.

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

[§]In this context we will take 'structural stability' to mean not only persistence of behavior for parameter changes in some neighborhood but also persistence of behavior within any class of models imbedding the current model.

2. THE MATHEMATICAL MODEL

The general developmental model for age, $a_j(t)$, within the j th life stage of a poikilothermic organisms can be written

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

The function $R_j(T)$ is the developmental rate, 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 (that is, $a_j(t_j) = 1$). A vast and growing literature is aimed at modelling and parameterizing the developmental rates, R_j , for various species as functions of temperature. This is simply because predicting the time of completion of the final life stage, t_N , for an N -stage organism is such an important applied problem. Formally, one may write the solution for t_N 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 rate curves and non-constant temperature series would probably necessitate computational approaches in any event.

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 is (following Taylor, 1981)

$$T(t) = T_0 - T_1 \cos(2\pi t). \tag{3}$$

In this equation T_0 is the yearly average temperature and T_1 is the size of the seasonal contribution to yearly temperature swings. The behavior of yearly temperature is *much* more complicated than this, but as will be shown below 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 for an $\frac{1}{m}$ -voltine cycle. Thinking of equations (2) as a circle map, the *rotation number*, ρ (or mean fractional rotation around the circle completed at each revolution) would be related to m by

$$\rho = \frac{1}{m}.$$

Unfortunately, irrational rotation numbers are much more frequent than rational rotation numbers, and there is no reason to expect simple cycles at the outset.

The final portion of the required mathematical formalism is an assumption for the shape of the rate curves. Over large temperature variations there is ample evidence that the rate curve for particular life stages depends nonlinearly on temperature [see Logan *et al.* (1976), and references quoted therein]. However, for an organism with many life stages the actual temperature experienced during a particular life stage varies less drastically. The simplest reasonable relationship that has been used to model developmental rate during a particular life stage is

$$R_j(T) = r_j(T - \theta_j) = r_j[T_0 - \theta_j - T_1 \cos(2\pi t)]. \quad (4)$$

In equation (4) 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 can be thought of as the developmental threshold temperature for life stage j . For simplicity we will assume throughout that $T_0 - T_1 \geq \theta_j$, so that the rate of aging never becomes negative. However, as we will show later, the argument for direct temperature control of seasonality is insensitive to truncating $R_j(T < \theta_j) = 0$. In the next section we will demonstrate how this argument proceeds for an organism with only two stages; egg and pre-ovipositional adult.

3. SYNCHRONIZATION IN AN ORGANISM WITH TWO LIFE STAGES

When we assume rate curves given by equation (4) and $N = 2$, equations (2) can be integrated directly,

$$1 = r_1 \left[(T_0 - \theta_1)(t_1 - t_0) - \frac{T_1}{2\pi} (\sin(2\pi t_1) - \sin(2\pi t_0)) \right],$$

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

To determine conditions for the existence of an m -cycle in oviposition we must examine these equations for solutions when $t_2 = m + t_0$. Taking m to be a positive integer (and therefore $\sin(2\pi(t_0 + m)) = \sin(2\pi t_0)$) gives

$$1 = r_1 \left[(T_0 - \theta_1)(t_1 - t_0) - \frac{T_1}{2\pi} (\sin(2\pi t_1) - \sin(2\pi t_0)) \right] \stackrel{\text{def}}{=} f_1(t_0, t_1), \quad (5)$$

$$1 = r_2 \left[(T_0 - \theta_2)(m + t_0 - t_1) - \frac{T_1}{2\pi} (\sin(2\pi t_0) - \sin(2\pi t_1)) \right] \stackrel{\text{def}}{=} f_2(t_0, t_1). \quad (6)$$

An $\frac{1}{m}$ -voltine cycle is given by intersections of the level curves $f_1(t_0, t_1) = 1$ and $f_2(t_0, t_1) = 1$.

In this case it is possible to solve analytically for t_0 . First, summing equations (5) and (6) with respective weights r_1^{-1} and r_2^{-1} yields

$$\frac{1}{r_1} + \frac{1}{r_2} = r_1^{-1} f_1 + r_2^{-1} f_2 = m(T_0 - \theta_2) + (\theta_2 - \theta_1)(t_1 - t_0). \quad (7)$$

From this equation we see that a *necessary condition* for the existence of a solution is $\theta_2 \neq \theta_1$, that is, that the life stages have different developmental thresholds. Otherwise we arrive at

$$m = \frac{1}{T_0 - \theta_2} \left(\frac{1}{r_1} + \frac{1}{r_2} \right),$$

which, since m must be an integer, cannot be true for general choices of T_0 , θ_2 and r_j .

When $\theta_2 \neq \theta_1$ we can solve for t_1 in terms of t_0 :

$$t_1 = t_0 + \frac{r_1^{-1} + r_2^{-1} - m(T_0 - \theta_2)}{\underbrace{\theta_2 - \theta_1}_{\stackrel{\text{def}}{=} \beta}}.$$

Using this definition for β , equation (5) becomes

$$\frac{1}{r_1} = \beta(T_0 - \theta_1) - \frac{T_1}{2\pi} [\sin(2\pi t_0 + 2\pi\beta) - \sin(2\pi t_0)],$$

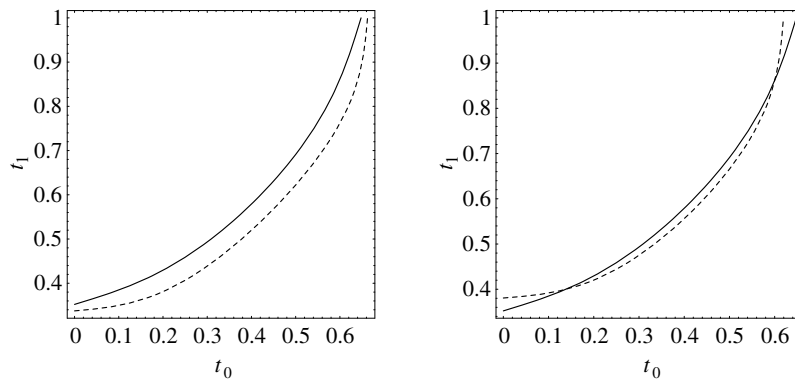


Figure 1. Transverse intersection and creation of fixed points in pairs for the two level curves $f_1(t_0, t_1) = 1$ (solid) and $f_2(t_0, t_1) = 1$ (dashed). The ovipositional date, t_0 , is the ordinate in each plot, while the date of egg hatching, t_1 , is the abscissa. Parameters were chosen to be $\theta_1 = 9$, $\theta_2 = 11$, $T_0 = 15$, $T_1 = 3.5$ and $r_1 = 0.6$. In moving from the figure on the left to the figure on the right only the parameter r_2 has been changed, from 0.32 on the left to 0.35 on the right. This illustrates the smooth movement of level curves with changing parameters and the consequent creation of two fixed points, given by the intersection between the two curves.

and using the cryptic trigonometric identity $\sin(x + 2y) - \sin(x) = 2 \sin(y) \cos(x + y)$ yields

$$\frac{1}{r_1} = \beta(T_0 - \theta_1) - \frac{T_1}{\pi} \sin(\pi\beta) \cos(2\pi t_0 + \pi\beta).$$

Finally, this expression may be inverted for t_0 :

$$t_0 = -\frac{1}{2}\beta + \frac{1}{2\pi} \cos^{-1} \left[\frac{\pi}{T_1} \csc(\pi\beta) \left(\frac{1}{r_1} + \beta(\theta_1 - T_0) \right) \right]. \tag{8}$$

In fact, equation (8) represents *pairs* of solutions in the interval $[0,1]$, since the cosine function intersects any constant value twice if it intersects at all in the interval $[0,2\pi]$. This is consistent with the behavior of intersections of level curves of two-dimensional functions. If it is possible that the level curves $f_1(t_0, t_1) = 1$ and $f_2(t_0, t_1) = 1$ *do not* intersect for some parameter values and intersections are created for other parameter values, then the intersections must be created in pairs (see Fig. 1). Moreover, the intersections created must be transverse intersections if the behavior of the level curves depends continuously on parameters. Since the functions f_1 and f_2 exhibit polynomial dependence on their parameters, the generic behavior of their level curves will be smooth with parametric changes. We conclude that fixed points will exist for neighborhoods of parameter values, that generically fixed points are transverse intersections of level curves, and are therefore structurally stable.

Recall that we are searching for ovipositional fixed points, t_0 , indicating seasonality, in what is essentially a circle map on the interval $[0,1]$, modulo 1. When isolated fixed points are created for circle maps (or iterations of circle maps), the fixed

points must be created in stable–unstable pairs (Guckenheimer and Holmes, 1983). While this result is the subject of theorems going back to Arnold and Avez (1968), intuitively it is fairly clear. Consider a sequence of ovipositional dates generated by integrating equations (2) recursively, starting with $t_0 \stackrel{\text{set}}{=} t_0^n$ and calculating the next generation's ovipositional date using $t_0^{n+1} = t_2 - m$ for an $\frac{1}{m}$ -voltine species. The sequence of ovipositional dates $\{t_0^n\}_{n=0}^\infty$ must contain a monotone convergent subsequence, $\{t_0^{n_k}\}_{k=0}^\infty$, because it is completely contained in the interval $[0,1]$. Without loss of generality, let us assume that this subsequence is increasing. The convergent subsequence must limit on a fixed point, and therefore one of the fixed points given by equation (8). Now consider the fate of eggs which are laid in any interval $[t_0^{n_k}, t_0^{n_{k+1}}]$. The future ovipositional dates for all initial conditions within the interval are trapped within future intervals $[t_0^{n_{k+j}}, t_0^{n_{k+j+1}}]$, and both interval endpoints converge to a fixed ovipositional date given by equation (8). Because the right-most endpoint of the last interval is the left-most endpoint of the next interval, a continuum of ovipositional dates must converge to what is an attracting ovipositional cycle. Since some ovipositional dates must converge from above and others from below, the second solution of the pair must be an unstable fixed point.

Finally, this behavior is structurally stable due to the transverse intersection which generates the fixed points (Guckenheimer and Holmes, 1983). As a consequence, 'nearby' similar systems will have the same properties for neighborhoods of their associated parameters. This holds true not only for two-stage organisms with nonlinear rate curves and more complex temperature series, but also for N -stage organisms in which the influence of all but two life stages is relatively small. This suggests that our results for two-stage organisms are generic, and that we can expect direct temperature control of seasonality in a spectrum of organisms. In addition, structural stability implies that the same organism should enjoy strong seasonality for a range of temperature regimes, including environments in which temperatures are not perfectly periodic. In fact, the results of simulations by Logan and Bentz (1999), using realistic temperature series, indicate that this is the case. The hypothesis that multi-stage organisms can experience direct control of seasonality will be examined in greater depth in the next section.

4. THE EXISTENCE AND STRUCTURAL STABILITY OF CYCLES FOR N -STAGE ORGANISMS

The situation for N life stages differs only in that no analytic solution is generally possible. However, given that the goal is only to exhibit the existence and structural stability of seasonal cycles this is not too great a handicap. To begin, using the linear rate hypothesis in equation (4) and the simple form for seasonal temperature

variation, each of the N equations (2) can be integrated directly:

$$\begin{aligned}
 1 &= r_1 \left[(T_0 - \theta_1)(t_1 - t_0) - \frac{T_1}{2\pi} (\sin(2\pi t_1) - \sin(2\pi t_0)) \right], \\
 &\vdots \\
 1 &= r_j \left[(T_0 - \theta_j)(t_j - t_{j-1}) - \frac{T_1}{2\pi} (\sin(2\pi t_j) - \sin(2\pi t_{j-1})) \right], \quad (9) \\
 &\vdots \\
 1 &= r_N \left[(T_0 - \theta_N)(t_N - t_{N-1}) - \frac{T_1}{2\pi} (\sin(2\pi t_N) - \sin(2\pi t_{N-1})) \right].
 \end{aligned}$$

An $\frac{1}{m}$ -voltine fixed oviposition cycle satisfies

$$t_N = m + t_0, \tag{10}$$

which gives a system of $N + 1$ equations with $N + 1$ unknowns, $t_0, t_1, t_2, \dots, t_{N-1}, t_N$. Thinking of equations (9) and (10) as level surfaces, the situation looks promising: if $(N + 1)$ surfaces intersect in an $(N + 1)$ -dimensional space they generically intersect transversely, at distinct points. In this section we will show that the surfaces intersect transversely for nontrivial circumstances.

Each of equations (9) can be written in the form

$$\frac{1}{r_j} = g_j(t_j) - g_j(t_{j-1}), \tag{11}$$

where

$$g_j(t) = (T_0 - \theta_j)t - \frac{T_1}{2\pi} \sin(2\pi t).$$

Provided

$$g'_j(t_j) = (T_0 - \theta_j) - T_1 \cos(2\pi t_j) \neq 0, \tag{12}$$

we may write a formal inverse for each life stage:

$$t_j = g_j^{-1} \left[\frac{1}{r_j} + g_j(t_{j-1}) \right]. \tag{13}$$

Condition (12) is satisfied by assuming $(T_0 - T_1) > \theta_j$, which means that the lowest yearly temperature stays above the developmental threshold for each life stage. This is no additional requirement at all; for the simple linear rate (4) to stay nonnegative we have precisely the same requirement.

Since the cosine function is always bounded between ± 1 we may write a bound on the derivative

$$\frac{d}{ds} g_j^{-1}[s] \leq \frac{1}{T_0 - \theta_j - T_1}. \tag{14}$$

It is now possible to determine a bound on the derivatives of G ,

$$\frac{dG}{dt_0} \leq \prod_{j=1}^N \frac{1}{T_0 - \theta_j - T_1}.$$

Therefore

$$\prod_{j=1}^N (T_0 - \theta_j - T_1) > 1$$

is sufficient to insure that $G'(t_0) < 1$ always.

Now we show that it is simultaneously possible for $G(0) > m$. Summing all N of equations (9) with weights r_j^{-1} and using equation (10) gives

$$\begin{aligned} \sum_{j=1}^N \frac{1}{r_j} &= t_N \cdot (T_0 - \theta_N) - t_0 \cdot (T_0 - \theta_1) + \sum_{j=1}^{N-1} t_j \cdot (\theta_{j+1} - \theta_j) \\ &\quad - \frac{T_1}{2\pi} [\sin(2\pi(m + t_0)) - \sin(2\pi t_0)]. \end{aligned} \tag{15}$$

We may isolate t_N on one side of equation (15) to get

$$t_N(T_0 - \theta_N) = t_0(T_0 - \theta_1) + \sum_{j=1}^N \frac{1}{r_j} + \frac{T_1}{2\pi} [\sin(2\pi(m + t_0)) - \sin(2\pi t_0)] - A,$$

where

$$A = \sum_{j=1}^{N-1} t_j \cdot (\theta_{j+1} - \theta_j).$$

If $A < 0$ we may write

$$t_N \geq t_0 \frac{(T_0 - \theta_1)}{(T_0 - \theta_N)} + \frac{1}{(T_0 - \theta_N)} \sum_{j=1}^N \frac{1}{r_j} + \frac{T_1}{2\pi(T_0 - \theta_N)} [\sin(2\pi(m + t_0)) - \sin(2\pi t_0)].$$

At $t_0 = 0$,

$$t_N \geq \frac{1}{(T_0 - \theta_N)} \sum_{j=1}^N \frac{1}{r_j} + \frac{T_1}{2\pi(T_0 - \theta_N)} \sin(2\pi m) \geq \frac{1}{(T_0 - \theta_N)} \sum_{j=1}^N \frac{1}{r_j}. \tag{16}$$

The latter inequality follows from m either an integer (so $\sin(2\pi m) = 0$) or $m \leq \frac{1}{2}$ (so $\sin(2\pi m) > 0$). Simply requiring the right-hand side of equation (16) to be greater than m at $t_0 = 0$ will satisfy condition (i).

The condition $A < 0$ is itself testable, but hard to express in biologically meaningful terms. However, consider the following. If we define the mean aging time, $\bar{t} = \frac{1}{N} \sum t_j$, then we may rewrite A :

$$A = \bar{t}(\theta_N - \theta_1) + \sum_{j=1}^{N-1} (t_j - \bar{t}) \cdot \Delta\theta_{j+1},$$

where $\Delta\theta_j = (\theta_j - \theta_{j-1})$ is the change in developmental threshold from the previous life stage. This quantity has zero mean, and consequently the summation term in A is proportional to the covariance of the t_j and $\Delta\theta_{j+1}$. Supposing for a moment that $\theta_N = \theta_1$, then life stages completing *before* the mean developmental time ($t_j < \bar{t}$) should coincide with *decreasing* jumps in developmental threshold ($\Delta\theta_{j+1} < 0$). Inversely, life stages completing *after* the mean developmental time ($t_j > \bar{t}$) should coincide with *increasing* jumps in developmental threshold ($\Delta\theta_{j+1} > 0$). Therefore, for a poikilothermic organism in which early life stages generally coincide with decreasing developmental thresholds and later life stages generally coincide with increasing developmental thresholds, we have shown that condition (i) is satisfied.

This is biologically relevant, since it is often empirically possible to determine the sequence of developmental thresholds for a particular organism. Mathematically it is not satisfying since the t_j are not explicit and, in fact, are part of the calculation for t_0 , which we are trying to show actually exists. However, it is clear that t_j is inversely related to r_j ; $T_0 - T_1 > \theta_j$ and equation (12) indicates that g_j has a positive derivative and equation (13) then shows that t_j must grow with r_j^{-1} . In fact, our earlier derivative estimates (14) give

$$t_j \leq t_{j-1} + \frac{r_j^{-1}}{T_0 - \theta_j - T_1} \leq \dots \leq \sum_{i=1}^j \frac{r_i^{-1}}{T_0 - \theta_i - T_1}.$$

Using this fact and telescoping the summation in A , we find

$$A \leq \frac{\theta_N - \theta_1}{r_1(T_0 - \theta_1 - T_1)} + \frac{\theta_N - \theta_2}{r_2(T_0 - \theta_2 - T_1)} + \dots + \frac{\theta_N - \theta_{N-2}}{r_{N-2}(T_0 - \theta_{N-2} - T_1)} + \frac{\theta_N - \theta_{N-1}}{r_{N-1}(T_0 - \theta_{N-1} - T_1)}.$$

This means that it is possible to bound $A < 0$ (and therefore use condition (16) to force $G(0) > m$) in a variety of ways. For example, suppose $\theta_j \approx \bar{\theta}$ except for a particular stage, k , for which $\theta_k \neq \bar{\theta}$. Then

$$A \leq \frac{\bar{\theta} - \theta_k}{r_k(T_0 - \theta_k - T_1)},$$

and $\theta_k > \bar{\theta}$ is sufficient to give $A < 0$. In fact, (16) becomes

$$G(0) > \frac{1}{(T_0 - \bar{\theta})} \sum_{j=1}^N \frac{1}{r_j},$$

and a sufficient condition for $G(0) > m$ in this case is just that

$$\frac{N}{\hat{r}} \stackrel{\text{def}}{=} \sum_{j=1}^N \frac{1}{r_j} > m(T_0 - \bar{\theta}). \tag{17}$$

As it turns out equation (17) also has a biological interpretation. The quantity \hat{r} is the *harmonic average* of the developmental times, and $(T_0 - \bar{\theta})$ is the mean temperature *in excess* of the averaged developmental threshold. Since m is the number of years in an ovipositional cycle and N is the number of life stages to complete, (17) is really a statement relating a particular kind of developmental averaging, the total temperature available for development in m years, and the number of life stages. That is, if we reorganize (17),

$$\underbrace{\text{‘Aging’ required}}_N = \underbrace{\text{Harmonic average rate}}_{\hat{r}} \times \underbrace{\text{Average temperature in } m \text{ years}}_{m(T_0 - \bar{\theta})}.$$

All that is required for such an organism to exhibit strong seasonality is that the harmonic average rate of development, \hat{r} , be great enough to complete all N life stages with the average available developmental temperature in m years.

It should be noted that nothing about this argument requires that m be an integer. For example, if $m = \frac{1}{2}$ then the conditions above are sufficient to determine whether or not an organism is bi-voltine. In fact, (17) can be used to distinguish bifurcations among a variety of possibilities. Taking T_0 to be a bifurcation parameter and \hat{r} to be given for a particular organism, then uni-voltine seasonality is predicted by (17) when

$$T_0 \simeq T_{1\text{-volt}} \stackrel{\text{def}}{=} \bar{\theta} + \frac{N}{\hat{r}}. \tag{18}$$

However, as the mean temperature increases it passes some critical temperature and enters a regime in which

$$T_{1\text{-volt}} < T_0 \simeq T_{2\text{-volt}} \stackrel{\text{def}}{=} \bar{\theta} + 2\frac{N}{\hat{r}}. \tag{19}$$

In the vicinity of $T_{2\text{-volt}}$ the theory predicts the existence of two generations per year, bi-voltinism. Clearly it is possible to extend the argument to predict regions of $k = \frac{1}{m}$ -voltinism:

$$T_{k\text{-volt}} \stackrel{\text{def}}{=} \bar{\theta} + k\frac{N}{\hat{r}}. \tag{20}$$

This provides a simple and direct method for predicting how seasonality may change as organisms spread to warmer/cooler latitudes or as the climate itself changes.

We have shown that fixed ovipositional cycles exist for simple linear development models for N -stage poikilothermic organisms and simple seasonal temperature dependence. Since the solution for t_0 is the result of transverse intersection of level curves it is structurally stable. We therefore expect strong seasonality in complex systems sufficiently similar to the simplistic system. It is not clear just how far 'sufficient similarity' can be pushed. Certainly more complex temperature cycles would not destroy the behavior we are analysing, provided the deviations from seasonal swings are not 'too' large. Nonlinear rate curves *would* be included if the nonlinearities are not 'too' extreme in the temperature regimes an organism experiences during its various life stages. Exactly what 'too' means cannot be determined at this point. However, direct temperature influences can certainly produce strict seasonality in an exothermic organism, independent of other synchronizing influences. In the next section we will show that this is, in fact, the case for the MPB.

5. APPLICATION TO MPB

The MPB (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) is a widely distributed native insect that attacks pine forests throughout the western United States. In general, a tree can only be colonized after a synchronized attack by hundreds or thousands of individuals. In addition to synchronous emergence, adults must maximize reproductive effort over the short time during which freezing temperatures do not occur in their mountain environments (Amman and Cole, 1983). These factors create a clear selective pressure for strict seasonality. Interestingly enough, in spite of extensive research and rearing experience with this species, no evidence for diapause or other physiological timing mechanism has been found (Wygant, 1942; Reid, 1962; Safranyik and Whitney, 1985; Logan and Amman, 1986). Rather, it seems as though seasonality is under direct temperature control. Due to their extensive geographical range, realistic mean temperatures for this species span the gamut of possibilities. Since there is no current evidence for diapause, the theory developed in the previous sections should predict a variety of seasonalities. Moreover, the actual phenology of MPB is much more complicated than the linear hypothesis we have used to develop the theory, as are the actual developmental temperatures encountered. Therefore, this species also provides an opportunity to determine the strength of the results presented above. Are these multi-voltine cycles structurally stable enough to exist for an organism with seven life stages, cool-temperature thresholds, and differing nonlinear and linear developmental rates in each life stage?

Nonlinear and linear development rate curve parameters for the seven MPB life

Table 1. Parameters for linearized rates of development for the MPB, including a developmental threshold, θ_j . Temperatures are measured in °C, while developmental rates r_j have units of inverse degrees per year.

Developmental stage	Developmental threshold	Linear rate
Egg	$\theta_1 = 7.5394$	$r_1 = 4.198$
First larval instar	$\theta_2 = 8.6358$	$r_2 = 10.695$
Second larval instar	$\theta_3 = 9.6322$	$r_3 = 10.439$
Third larval instar	$\theta_4 = 8.0342$	$r_4 = 3.468$
Fourth larval instar	$\theta_5 = 10.9543$	$r_5 = 3.650$
Pupae	$\theta_6 = 11.7555$	$r_6 = 6.278$
Ovipositional adult	$\theta_7 = 1.7929$	$r_7 = 1.278$

stages were estimated previously (Logan and Amman, 1986; Bentz *et al.*, 1991; Logan and Bentz, 1999) (see Fig. 3). To apply the theory developed above, we linearize the nonlinear rate curves and estimate a lower temperature threshold for development (see Table 1). 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 development thresholds for this insect are those derived from the nonlinear rate curves. Our goal in this section is to examine the predictions of the theory developed in the previous section, not to re-create the actual phenological attributes of the MPB's life cycle.

Structural stability will be examined in two generalizations of the linear, above-threshold developmental model. In the first case, the development with linearized rate curves (including developmental thresholds) will be examined for temperatures passing below developmental thresholds. This will show that introducing realistic developmental thresholds does not destroy the stability of seasonality analysed above (in fact it strengthens seasonality). In the second case we use the fully parameterized, nonlinear development curves to illustrate that the nonlinearity of the rate curves does not remove seasonality. The empirical rate curves corresponding to (2) are integrated numerically using the trapezoid rule with hour-long time steps, generating ovipositional dates for the next generation (t_N) as a function of ovipositional dates in the current generation (t_0). The full MPB model is the same as that used in Logan and Bentz (1999). By simply iterating the ovipositional map for many generations we are able to determine which seasonal cycles, if any, are attracting.

Temperatures will be modelled using a truncated Fourier series (following Taylor, 1981)

$$T = T_0 - T_1 \cos(2\pi t) - T_{365} \cos(730\pi t). \quad (21)$$

The behavior of the phenology model will be examined as the energy in the mean

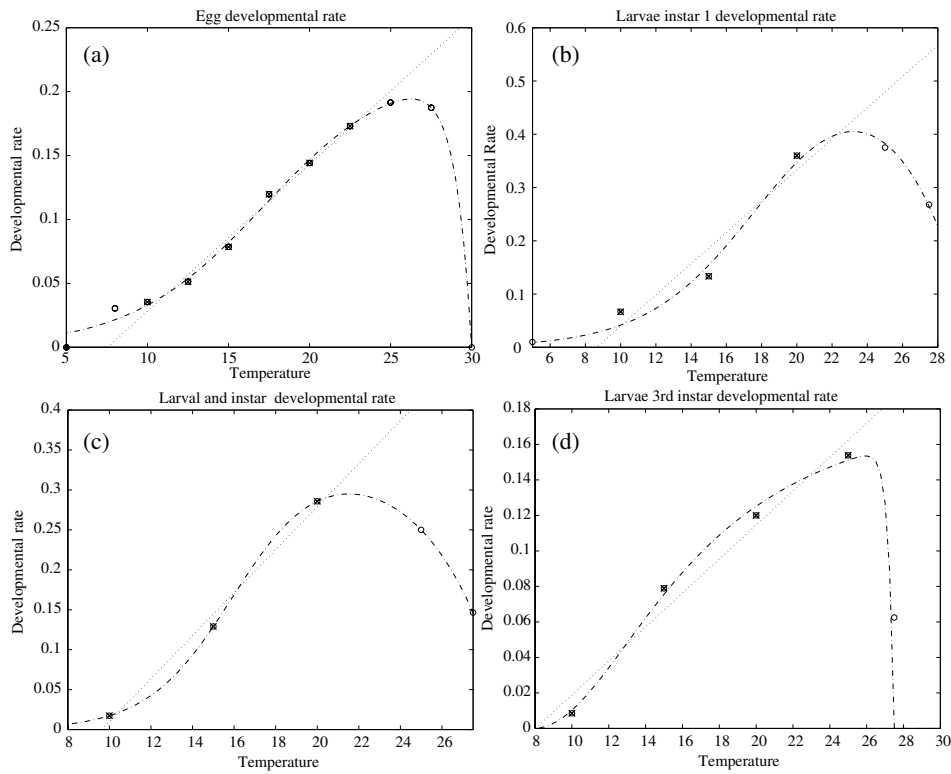


Figure 3. Actual estimated rate curves for MPB (solid) and simple linear approximations (dashed) with developmental thresholds and linear rates of development. From left to right, top to bottom the curves represent rates of development for: (a) eggs, (b) first larval instar, (c) second larval instar, (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 parameterize a purely linear representation of the developmental rate.

(T_0), seasonal (T_1) and daily (T_{365}) temperature modes is varied. A particular example of such a temperature series is shown in Fig. 4.

The numerical case studies will be organized by the conditions for k -voltinism discussed in the previous section. For MPB the two averaged quantities, \hat{r} and $\bar{\theta}$ are

$$\hat{r} = 3.62325 \text{ (}^\circ\text{C-year)}^{-1} \quad \text{and} \quad \bar{\theta} = 8.33483 \text{ }^\circ\text{C}.$$

Using equation (20) with $N = 7$ generates predictions for seasonality, which are summarized in Table 3. Predicted temperatures range from 9.3 °C for a semivoltine cycle to 20 °C for hexavoltine seasonality. In general the parameters for the MPB ‘pass’ the qualitative criteria discussed in the previous section. In particular, the pupal stage has a developmental threshold with highest positive deviation from the mean threshold, $\bar{\theta}$. Consequently we expect that a variety of seasonalities will be possible for the MPB life system.

Of the seven temperature regimes in Table 3, the semi-, uni- and bi-voltine cases

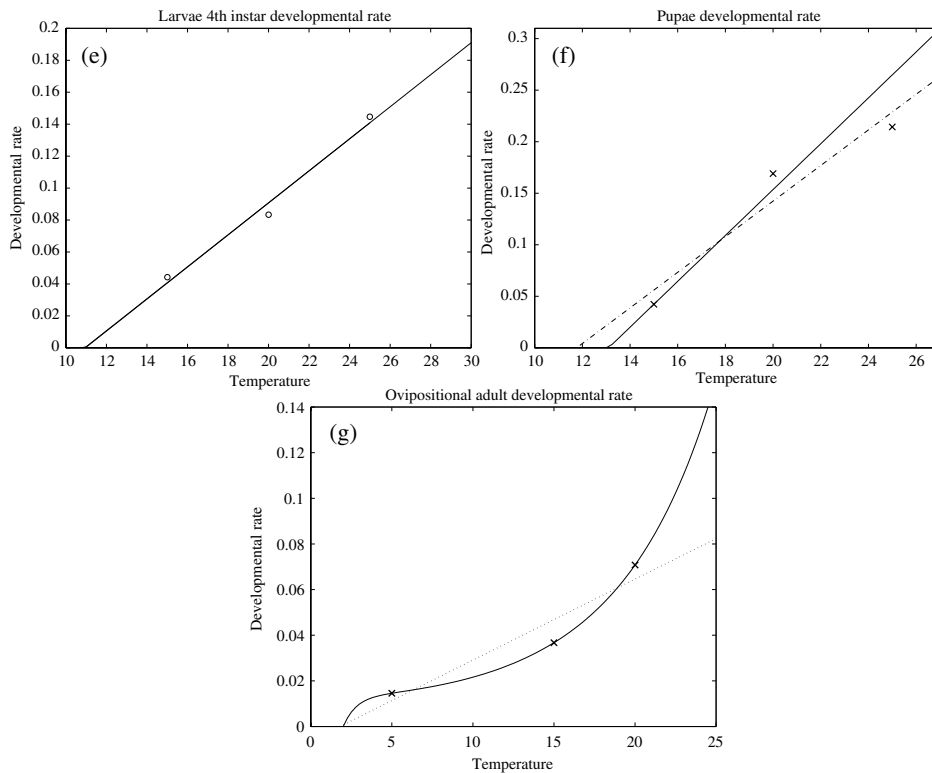


Figure 3. Continued.

are not relevant to the simple linear theory. In each of these cases the mean temperature threshold is below the highest developmental threshold ($\theta_6 = 11.75$). Consequently our investigations below will be conducted in a high mean-temperature regime; unrealistically high, from the standpoint of the actual temperature environment experienced by the MPB. However, the goal of this work is not to predict seasonality for MPB, but to establish that temperature alone is sufficient to synchronize the life cycles of poikilothermic organisms. The MPB is simply a test-case with established rate curves, thresholds, and lack of diapause.

5.1. Linear rates and realistic development thresholds. To examine the structural stability of the predicted seasonality under the influence of true developmental thresholds we integrated equation (1) with linear rates and thresholds as depicted in Fig. 3. The mean yearly temperature was chosen to be $T_0 = 14.2$, squarely in the regime of tri-voltine cycles. Seasonal and daily temperatures were chosen in the ranges $T_1 \in [2, 10]$ and $T_{365} \in [2, 8]$. The computational model was integrated with arbitrarily chosen initial conditions for at least 100 generations of developmental time, and the sequence of oviposition dates were examined for seasonality. For each choice of T_1, T_{365} the number of generations per year at the end of the

Table 2. Functional forms and parameters for the nonlinear developmental rate curves for MPB [following Logan (1988)]. Graphical versions are plotted in Fig. 3. The four larval instars are indicated by 'L_{1,2,3,4}'. Parameters were estimated using observations discussed in Logan and Bentz (1999). For temperatures at which the given functions become negative the rate of development is taken to be zero. In the case of the third larval instar, $R_4(T) = 0$ for $T < 7.9046$. Developmental rates (p_1) are given in units of per year, per °C; other parameters are directly proportional to °C or inverse °C, as appropriate.

Stage	Functional form	p_1	p_2	p_3	p_4	p_5
Egg	$p_1 \left(\frac{1}{1 + p_2 \exp[-p_3(T - 5)]} - \exp \left[\frac{(T - p_4)}{p_5} \right] \right)$	114.90	19.93	0.20	34.60	4.89
L ₁	$p_1 \left(\frac{1}{1 + p_2 \exp[-p_3(T - 5)]} - \exp \left[\frac{(T - p_4)}{p_5} \right] \right)$	251.38	57.28	0.30	30.22	4.60
L ₂	$p_1 \left(\frac{1}{1 + p_2 \exp[-p_3(T - 10)]} - \exp \left[\frac{(T - p_4)}{p_5} \right] \right)$	130.01	18.01	0.48	29.36	3.47
L ₃	$p_1 \left(\frac{(T - p_5)^2}{p_4^2 + (T - p_5)^2} - \exp \left[\frac{(T - p_2)}{p_3} \right] \right)$	69.68	19.70	0.15	8.77	7.90
L ₄	$p_1(T - p_2)$	3.65	10.95			
Pupae	$p_1(T - p_2)$	6.28	11.76			
Adult	$p_1 \left(\exp[p_2(T - p_4)^{p_3}] - \exp \left[\frac{(T - p_4)}{p_5} \right] \right)$	4.90	0.019	1.54	2.00	0.80

simulation (possibly large) were recorded. A contour plot of these seasonalities is presented in Fig. 5. The region of tri-voltinism extends well past the threshold developmental temperatures, which illustrates the structural stability of the theoretical predictions. In general, one may hypothesize that the cycles are eventually de-stabilized by the high temperatures during the summer, which in the end put so much developmental energy into the system that 3 generations per year are simply too few, generating a temperature regime of a-synchronous fractional voltinism. Eventually, as temperatures are increased still further, a 4-generation per year set of cycles become stable and attracting, as indicated in the figure.

5.2. Nonlinear rates. To examine the structural stability of the predicted seasonality under the influence of nonlinear rate curves as well as realistic developmental thresholds we integrated equation (1) with nonlinear rates and thresholds as depicted in Fig. 3. The mean yearly temperature was chosen to be $T_0 = 14.2$, squarely in the regime of tri-voltine cycles. Seasonal and daily temperatures were chosen in the ranges $T_1 \in [2, 8]$ and $T_{365} \in [2, 10]$. The computational model was integrated with arbitrarily chosen initial conditions for at least 100 generations of developmental time, and the final 50 generations were examined for seasonality. For each choice of T_1, T_{365} the number of generations per year at the end of the simulation (possibly large) were recorded. A contour plot of these seasonalities is

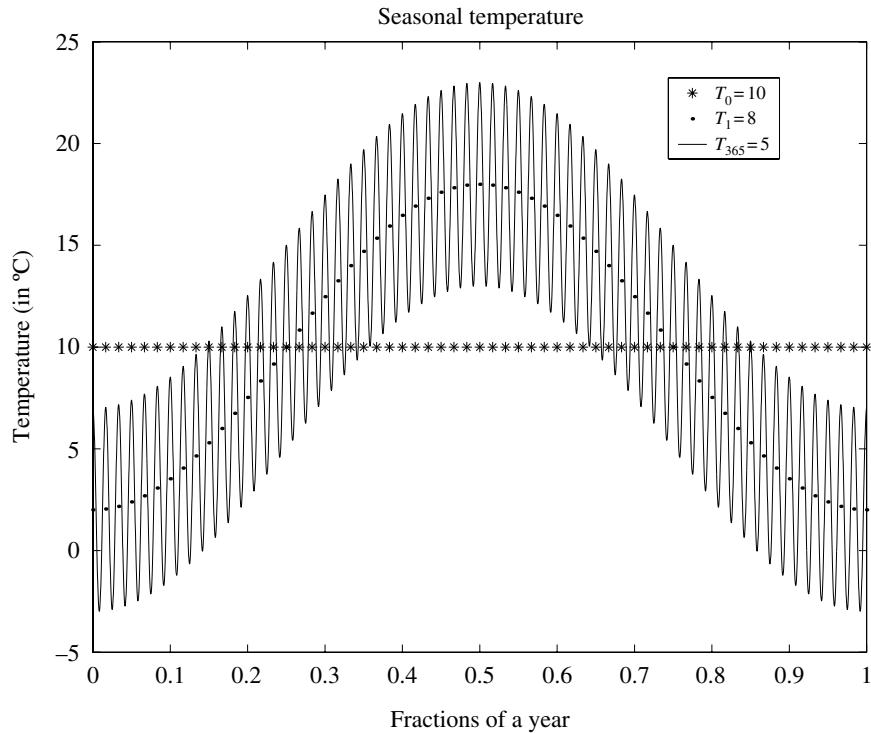


Figure 4. Example temperature series $T = T_0 - T_1 \cos(2\pi t) - T_{365} \cos(730\pi t)$ including mean (*, $T_0 = 10$), seasonal (·, $T_1 = 8$) and daily (—, $T_{365} = 5$) temperature components. In the numerical studies the seasonal (T_1) and daily (T_{365}) components of temperature are varied (independently) so that the total temperature drops below developmental thresholds. The independent axis, t , is measured in fractions of a year after the minimum seasonal temperature.

presented in Fig. 6. In this figure it is clear that there are two basic seasonalities, a tri-voltine ($k = 3$) cycle as well as a quadri-voltine ($k = 4$) cycle. These are the basic seasonalities exhibited by the linear developmental model in the same temperature regime. The continued existence of cycles in the case of nonlinear curves and realistic developmental thresholds illustrates that cycles predicted by the linear, no-threshold theory are structurally stable. It is interesting to note that daily fluctuations stabilize the expression of seasonality, as indicated by the concavity of the bands of adaptive seasonality.

5.3. Discussion. The purpose of the two case studies presented above is to illustrate the structural stability of the cycles proven to exist in the linear rate, no-threshold model. In fact the cycles persist nicely in both linear and nonlinear cases when thresholds are included. In both cases we studied a very high-temperature regime, to facilitate comparison with the no-threshold theory. One might expect that here cycles would be *least* stable—there is too much developmental energy

Table 3. Mean yearly temperatures which result in differing numbers of generations per year for the MPB, using linear rate curves and parameters summarized in Table 1.

Generations/year, k	$m = \frac{1}{k}$	Mean temperature, $T_{k\text{-volt}}$
1/2	2	9.3008
1	1	10.2668
2	1/2	12.1988
3	1/3	14.1307
4	1/4	16.0627
5	1/5	17.9947
6	1/6	19.9266

around for simple cycles to stay stable. In a low-temperature regime numerical investigations [see Logan and Bentz (1999), for details] indicate patterns of semi-, uni- and bi-voltine cycles that are structurally similar to the results we present here. On the basis of the theory discussed above this seems reasonable. When the temperature goes below threshold no development occurs, corresponding to the region in which $G'(t_0) = 0$. Since the existence and stability of cycles hinges on the notion of making the average slope of G smaller than one, it seems clear that developmental thresholds should strengthen, rather than weaken, cycles.

The boundaries of the two regions displaying tri- and quadri-voltine cycles in Figs 5 and 6 are quite complicated. While the figures were plotted using discretizations of 0.2 °C, we have used discretizations as small as 0.05 °C in selected regions including the boundaries and the complications persist or increase. It may be that these boundaries are essentially fractal, although we have not begun to perform enough simulations to test this hypothesis. The reasons for this complication are tied to the existence of true developmental thresholds in both the linear and nonlinear models. The function $t_N = G(t_0)$, which describes the time of completion of the final (N th) life stage in terms of oviposition time (t_0), need not be continuous when temperatures pass through a developmental threshold. To see this, imagine the developmental trajectories of two eggs laid one day apart. Suppose the first egg just completes development the day before temperatures pass through the threshold for egg development. The second egg will be halted before it completes development, and will not hatch until somewhat later in the year, when temperatures rise back through the egg's developmental threshold. In the meantime, the first egg has made it into later instars which may or may not have developmental stops. In any event, the trajectories of these two eggs have diverged, perhaps by as much as an entire half year, in spite of their initial proximity. Thus, when temperatures pass through thresholds $G(t_0)$ does not need to be continuous. A direct consequence of this fact is that the voltine boundaries, which are smooth for temperatures staying above threshold, do not continue smoothly when temperatures fall through the developmental thresholds.

The areas of asynchronous, fractional voltinism resulting from both the linear

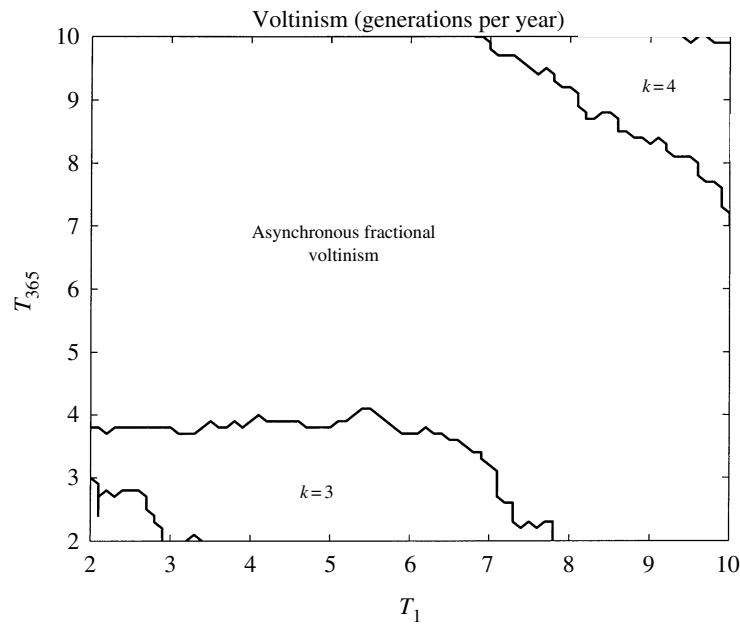


Figure 5. Numerically calculated seasonality for linear rate curves with realistic developmental thresholds. The mean temperature is $T_0 = 14.2$; daily (T_{365}) and seasonal (T_1) temperatures vary from 2 to 10 and 2 to 10, respectively. Except for the lower left corner of the plot all temperatures pass below developmental thresholds. The region of tri-voltinism (with $k = 3$) persists well beyond where temperatures cross the threshold, illustrating the structural stability of the three cycles. For larger T_{365} and T_1 a region of quadri-voltinism also exists. These two regions of synchrony are separated by a region in which ovipositional cycles were not an integer number per year, indicating asynchronous fractional voltinism for these temperature regimes.

and nonlinear case studies (see Figs 5 and 6) can be interpreted as phase transitions that are maladaptive for this insect. These areas represent transition zones between strict uni-, bi- and multi-voltinism in which population synchrony is disrupted, thereby possibly limiting population expansion [see Logan and Bentz (1999)]. These and similar results will be pursued in future work.

6. CONCLUSION

In this paper we have proven that it is possible for seasonal temperature variation, coupled with differing developmental thresholds for different life stages, to synchronize the seasonality of a poikilothermic organism. The two basic conditions under which direct temperature control creates seasonality are: (1) that sufficient developmental energy exists to move through N life stages in a season (half- or two-seasons, as the case may be), and (2) that at least one of the developmental thresholds is significantly above the mean threshold, $\bar{\theta}$. These two general criteria

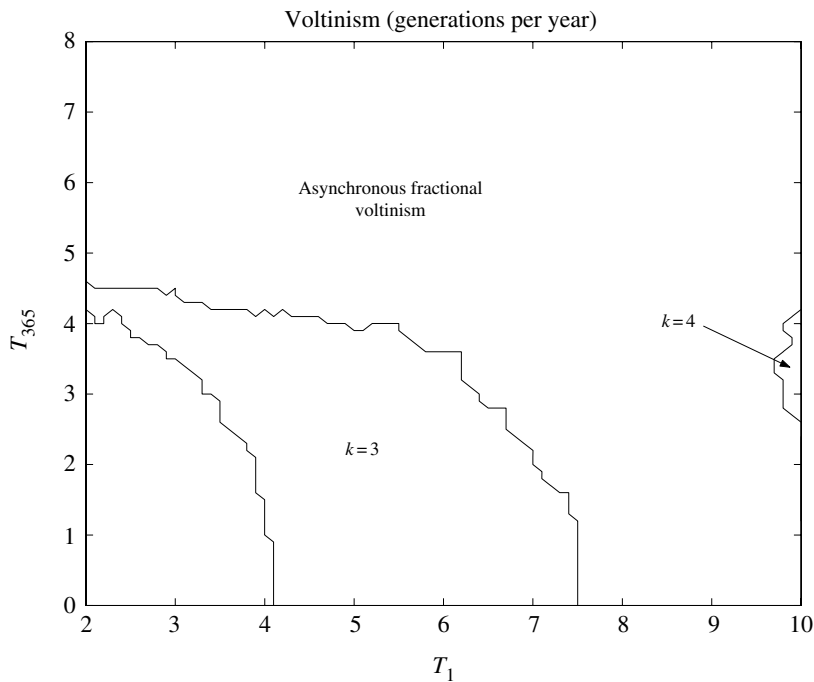


Figure 6. Numerically calculated seasonality for nonlinear rate curves with true developmental thresholds. The mean temperature is $T_0 = 14.2$; daily (T_{365}) and seasonal (T_1) temperatures vary from 0 to 8 and 2 to 10, respectively. Except for the lower left corner of the plot all temperatures pass below developmental thresholds. Regions of adaptive seasonality (in this case a tri- and quadri-voltine band) are separated by bands of asynchronous fractional voltinism.

determine conditions under which seasonal temperature variations will create fixed points in the generational circle map from ovipositional date to ovipositional date.

There are many suggestive implications of this theoretical result. Many organisms exhibit no obvious physiological timing mechanism (such as diapause, hibernation, or estivation), yet pursue life strategies which make them dependent on synchrony with conspecifics. Examples are as various as terrestrial and aquatic insects, pollinating plants, bacteria and fungi, amphibians and fish. It is often hypothesized that some unknown environmental cue and physiological mechanism provides the biofix. A more parsimonious explanation may be direct temperature control of seasonality. Nobody doubts that rates of development vary with different life stages and different temperatures, nor that there are thresholds for each life stage below which no development occurs. In this paper we have demonstrated that these mechanisms *alone* are sufficient to create voltinism in the presence of seasonal temperature variations, and that the resulting cycles are very stable.

ACKNOWLEDGEMENTS

This work was supported by the USDA Forest Service Mountain Pine Beetle Project through grant number RMRS-99612-RJVA.

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Received 3 January 2000 and accepted 30 April 2000