

Model Analysis of Mountain Pine Beetle (Coleoptera: Scolytidae) Seasonality

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ABSTRACT The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a natural disturbance agent of considerable consequence in western pine forests. This economically and ecologically important insect has a strong requisite for maintaining a strict seasonality. Given this ecological requirement, it is somewhat surprising that no evidence for diapause or other physiological timing mechanism has been found. Seasonality and phenological timing for this species are apparently under direct temperature control. We investigate the consequences of direct temperature control by first constructing a computationally efficient phenology model based on previously published temperature dependent developmental data. We explored the dynamic properties of this model when subjected to observed microhabitat temperatures representing a range of thermal habitats from one region of the mountain pine beetle distribution. We also investigated the consequences of global climate change on phenology and seasonality. Our results indicate that an adaptive seasonality is a natural consequence of the interaction between developmental parameters and seasonal temperatures. Although this adaptive phenology appears to be resilient to temperature fluctuations, changes in climate within the magnitude of predicted climate change under a CO₂ doubling scenario are capable of shifting a thermally hostile environment to a thermally benign environment. Similarly, increasing temperature by the same amount resulted in phenological disruption of a previously favorable thermal habitat. We discuss the implications of these results for restricting the current distribution of mountain pine beetle, and the potential for shifting distribution caused by global climate change.

KEY WORDS mountain pine beetle, direct temperature control, phenology, seasonality, climate change, temperature-dependent development

MAINTAINING AN APPROPRIATE seasonality is one of the most important requisites for insects living in temperate environments. Critical life-history events must be appropriately timed with seasonal resource abundance. Additionally, successful adaptation to times of seasonal stress (e.g., winter, dry season) often require timing of a particular life stage to correspond with seasonal environmental cues. Temperature is the most basic controller of seasonality in poikilothermic organisms (Zaslavski 1988). Information relating developmental rates, and subsequently seasonality, to temperature exist in the literature for literally hundreds of insect species. In this large body of work, mathematical models used to predict phenology and seasonality have been particularly successful, perhaps being the most widespread and useful entomological application of mathematical models. These applications have proven useful in applied entomology for improved timing of control applications, as well as in more basic ecological research.

Models of phenology often require some starting point where essentially all members of the targeted population are the same age. This biofix has often been the breaking or termination of diapause. Diapause itself is typically temperature related, and is an almost universal adaptation by terrestrial insects to maintain an adaptive seasonality. It has been argued, in fact, that diapause is an early evolutionary adaptation of insects because of its almost universal expression (Zaslavski 1988). Some insect species, however, exhibit no obvious manifestation of diapause. Whether or not this is a secondary loss of the capacity for diapause is an interesting question, but regardless of the answer, some temperate insect species maintain an appropriate seasonality without diapause to synchronize their life cycle. Maintaining seasonality without some obvious physiological mechanism, such as diapause, to reset the seasonal clock has been termed direct control of seasonality (Danks 1987).

Extensive rearing experience with mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in our laboratory and others has failed to indicate diapause for this species. Winter-collected, or chilled individuals, resume development immediately on warming (Wygant 1942, Logan and Amman 1986). Individuals

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collected from the field in summer can be reared through to adult without chilling (Reid 1962, Safranyik and Whitney 1985). No apparent differences in developmental rates are observed between individuals held in cold storage from those reared directly from field collections (B.J.B., unpublished data). At this time, seasonality for this species must be considered as being under direct temperature control, or at the very least, no timing mechanism other than direct control has been found.

Lack of a timing mechanism, like diapause, for maintaining seasonality in mountain pine beetle is somewhat surprising because this species has a strong ecological requisite for strict seasonality. The first requirement is for an emergence time that is late enough in the summer to avoid lethal freezing temperatures, but early enough in the season to achieve full ovipositional potential before lethal fall/winter temperatures. Second, the mountain pine beetle is a predator (rather than a parasite) that must kill its host to successfully reproduce (although partial or strip attacks on trees sometimes occur). Pine tree hosts are far from passive victims, and substantial defenses have evolved to protect potential hosts (virtually all *Pinus* species) from beetle attack. In response to these defenses, mountain pine beetles have evolved a mass attack strategy that overwhelms the tree by sheer number of attacking beetles. The second phenological requisite is, therefore, synchrony of adult emergence to provide the maximum number of beetles required for this strategy. In the remainder of this article, we use the term *seasonality* in reference to an adult ovipositional period that meets the first requirement, and the term *synchrony* for the latter.

The ecological requirements for seasonality and synchrony raise interesting questions. In field observations (mountainous environments with a limited warm season), appropriate seasonality has been associated with univoltinism. Population performance is severely compromised when a 1-yr life cycle is interfered with, for example at high elevations or northern latitudes lacking sufficient thermal input (Amman 1973, Safranyik 1978). The question in this regard is how to maintain an appropriate seasonality without diapause. Bentz et al. (1991) explored this issue for one particular case. They concluded that the relationship between developmental thresholds for the various larval instars and predictable winter temperature could result in an appropriately timed emergence. The central issue regarding synchrony is how an initial distribution of several months oviposition is focused onto an adult peak emergence that lasts only 1–2 wk. Logan et al. (1998) demonstrated the importance of focusing emergence, but they provided no mechanistic insights. We expanded on the ideas of Bentz et al. (1991) and Logan et al. (1998) by testing the dynamical properties of timing under a broader range of environmental conditions. Magnuson et al. (1979) considered temperature an ecological resource in the same sense of any other critical component of the habitat. In this article we explore the issue of direct temperature control of seasonality and synchrony. We

then address the potential implications of changing global climate for this economically and ecologically important species.

Materials and Methods

Model Development. Phenology models have been used for a variety of applications, ranging from timing of insect control strategies, to more theoretical, inferential applications of hypothesis generation and testing in ecological research. The goal of the model we discuss is to provide a means for exploring effects of weather and climate on mountain pine beetle seasonality. In this respect, our application is similar to a laboratory experiment in that the idea is not to recreate nature, but rather to isolate an important component from the real-world environment in a way that allows experimental manipulation. To provide an effective experimental tool, our model must provide a rational representation of the phenomena and it must respond in a reasonable fashion. Finally, because we are interested in characterizing the general, qualitative response of mountain pine beetle seasonal adaptation to weather, we will consider predicting the median as a first approximation of the population response.

The basis for most insect phenology models is the developmental rate curve. Developmental rate (the inverse of time required to complete a stadium) is expressed as a function of temperature. Over the full range of thermal response, the developmental rate curve has been found to be nonlinear and asymmetric about the optimum temperature, with precipitous decline following the optimum (Logan et al. 1976). Nonlinearity and asymmetry result in difficulties simulating insect phenology. First, as true for nonlinear curves in general, the average developmental rate for variable temperatures is not equivalent to the developmental rate at the average temperature (Allen 1988). This discrepancy is further accentuated by asymmetry about the thermal optimum. Therefore, using mean daily temperatures can result in substantial errors, and a smaller time-step, such as hourly temperature, is required.

Confounding the requirement for high temporal resolution is the necessity for running the model many and perhaps thousands of times to draw inferences about the effects of weather and climate on seasonality. This requirement arises from 3 sources. First is the difficulty in interpreting temperature patterns. It is easy, given modern technology, to remotely monitor microhabitat temperatures. The difficulty lies in interpreting this complex circadian and circannual signal in ecological terms (Amman 1985). Use of a model has proven invaluable for supplying the ecological filter for this interpretation. Second is the dynamical complexity that is inherent in nonlinear phenomena (Logan and Allen 1992). Advances in dynamical systems theory over the past 20 yr have provided a rich conceptual basis for investigating behavior of nonlinear phenomena, but this basis is largely founded in mathematical empiricism that re-

quires extensive numerical solution and simulation. The third reason arises from the nature of climate and climate change. For such issues, we are interested in investigating phenomena that occur over long time frames, perhaps hundreds of years, and it is necessary to perform simulation over these extended periods. The requirement for high temporal resolution combined with questions that are inherently computationally intensive provides the motivation for developing a realistic phenology model that runs efficiently on readily available personal computers.

We have developed a C-code model for mountain pine beetle phenology (Logan et al. 1995) based on the algorithms in Logan (1988) and parameter values in Bentz et al. (1991). This model (MPBMOD) is relatively efficient with 1 simulation year requiring ≈ 1 min CPU time on a Pentium Pro 200 level PC. However, for applications that require running the model thousands of times, even this level of computational overhead becomes intolerable. We have therefore restructured a less complex model in the MATLAB (Math Works 1998) mathematical language.

The phenology model is based on a 2 step process. First, an entire year of developmental indices (the proportion of the life stage completed each j th day for each i th life stage) is computed as

$$D_{ij} = \sum_{k=1}^{24} f(T_k; \underline{p}_i) / 24, \quad [1]$$

where j equals 1–365 for 1 yr, f is a user defined developmental rate function with arguments temperature T (hourly temperatures) and parameters \underline{p}_i . The result is divided by 24 because the developmental rate equation is solved for hourly temperatures and aging is computed on a daily time step. Second, for each life stage in the model, the median day of emergence for each i th instar is computed by solving the summation equation for n_day ,

$$1 = \sum_{j=day_start}^{n_day} D_{ij}, \quad [2]$$

from beginning day day_start to median emergence day n_day . The full phenology is simulated by cascading through equation 2 for each life-stage, with the n_day for 1 life-stage becoming the day_start for the next. MATLAB code for the mountain pine beetle simulation model is included in Appendix 1.

Model Parameterization. Immature Development. Parameters for egg developmental rate are listed in Logan and Amman (1986), with the addition of a low temperature developmental threshold of 5°C (Reid and Gates 1970). Developmental rate equations and parameters for larval instars are listed in Bentz et al. (1991). The developmental rate equation for teneral adults was derived from experiments that were conducted in phloem sandwiches (as described in Bentz et al. 1991). Constant temperature experiments were conducted at 6 temperatures, ranging from 10 to 25°C. The lower threshold for pupation to the teneral adult

stage was found to be between 15 and 17.5°C. The resulting developmental rate equation is modeled as Stinner's (Stinner et al. 1974) developmental rate curve,

$$r(T) = p_1 / (1 + e^{p_2 + p_3 T})$$

$$\tau = T \text{ for } T \leq p_4; \quad \tau = 2p_4 - T \text{ for } T > p_4,$$

for $p_1 = 0.11912$, $p_2 = 93.926$, $p_3 = -5.277$, and $p_4 = 24.06$. The developmental rate function for teneral adults is interesting in that it is essentially temperature insensitive for all but the lowest temperatures. This is consistent with field observations that the duration of the teneral adult stage is largely controlled by feeding (Six and Paine 1998, Bentz and Mullins 1999).

Ovipositional Adult. Adult development (longevity) is modeled through egg gallery production as a function of temperature. The basic equation is given as equation 1 in Logan et al. (1995), and is based on data from Amman (1972) and Reid (1962). Median adult longevity is considered to be the time when the median value of the ovipositional curve is reached (i.e., 32 cm, the gallery length at which the median egg is oviposited), this projected time is termed *median adult*. To achieve consistent results, all simulations were conducted from date of median adult (generation n) to median adult (generation $n+1$).

In our opinion, the described model is the most up-to-date and complete mechanistic model of mountain pine beetle temperature-dependent development. In other words, it represents the current state-of-the-art knowledge for mountain pine beetle phenology.

Temperature Data Sets. Through a variety of studies, some published (Bentz 1995, Bolstad et al. 1996, Bentz and Mullins 1999) and others in progress, we have acquired a large number of data sets monitoring mountain pine beetle microhabitat temperatures. Procedures for recording temperature are fully described in Bentz and Mullins (1999), but briefly consist of inserting a chromega/constantan thermocouple into the phloem tissue and recording average hourly temperatures from a 1 min sampling interval.

All reported temperature data came from the Stanley Basin in north central Idaho. Experimental sites are in the Sawtooth National Recreation Area, Lat. 44° 07' N, 114° 52' E and at an approximate elevation of 2,050 m. The Stanley Basin has been undergoing a low-intensity sub-outbreak for the past 11 yr. Although a broad band of suitable host material (even-aged stands of susceptible lodgepole pine) exists in this area, populations are maintained at a moderate (rather than outbreak) level, presumably because of a sub-optimum climate that is often too cold during critical times of the year. The following 4 annual temperature data sets from this area were used: (1) Averaged phloem temperatures from north and south aspects of 3 mountain pine beetle infested lodgepole pine trees growing on a southwest aspect site. This site is in a relatively warm microhabitat, and will be referred to as *warm-averaged* temperature. (2) Averaged phloem temperatures from north and south aspects of 3 mountain

pine beetle infested lodgepole pine trees growing on a northeast aspect site. This site is in a cold microhabitat that we will refer to as *cold-averaged* temperature. (3) Phloem temperature measurements from an individual thermocouple on the south aspect of an infested lodgepole pine growing on a southwest aspect site. These temperatures are the *warm-specific* data. (4) Phloem temperature measurements from an individual thermocouple on the north aspect of an infested lodgepole pine growing on a southwest aspect site. This temperature profile is the *cold-specific* data.

Because we are investigating temperature effects on seasonality, including the possibility of semivoltinism, we created multiyear temperature records for each data set by simply repeating the annual temperature cycle.

Results

Temperature. The warm-averaged and cold-averaged temperatures were recorded from August 1995 to August 1996, years with weather typical of the area climate. The warm-specific and cold-specific data were recorded from August 1992 to August 1993. In 1993 it was cooler than average, including the coldest average monthly July temperature during the period of record 1895–1997 (NOAA, NCDC Regional Summary Data, Idaho Region 8). The warm-averaged site was the warmest with an annual mean temperature of 3.72°C (standard deviation 9.73) and 2,129 degree-days (DD) above base 0, followed by the cold-averaged site with an annual mean temperature of 2.60°C (standard deviation 10.58) and 1,940 DD above base 0, next was the warm-specific site with a mean annual temperature of 2.17°C (standard deviation 10.20) and 1,895 DD above base 0, the cold-specific site was coldest with a mean annual temperature of 1.79°C (standard deviation 9.77) and 1,708 DD above base 0. Temperature profiles are shown in Fig. 1 to indicate the magnitude of daily temperature variation as well as the degree of differences between the temperature data sets.

Description of Simulations. The 3 central issues regarding seasonality in mountain pine beetle are as follows: (1) Does “typical” weather acting on the independently derived phenology model result in a reasonable (adaptive) seasonality? (2) How resilient is the model to variation in weather patterns? (3) What are the stability properties of mountain pine beetle seasonality? To address these questions, we monitored the dynamical properties of the system for multi-year simulations for the 4 weather data sets. Because the basic issues we are interested in center on the ability of phenology to focus critical seasonal events, we initiate the model with the most dispersed distribution possible (i.e., an egg oviposited on each day of the year). We then follow the resulting phenology of each initial condition over a period of several years with the predicted median oviposition date from 1 yr providing the initializing oviposition dates for the next year. Because each year’s weather is an exact replica of the previous year, final median adult dates were reduced

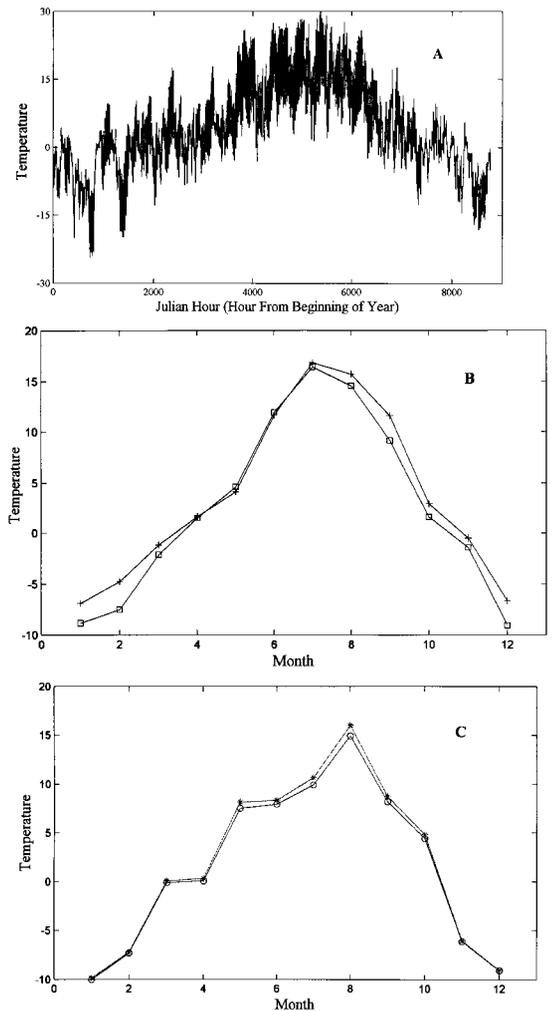


Fig. 1. (A) Hourly temperature for the cold-average site. (B) Monthly average temperature for both average sites. (C) Monthly average temperature for both specific sites.

by modulo 365 (the remainder in days after dividing by 365) to initiate the next year’s simulation.

An easier and more convenient way to express the dynamic properties of seasonality is to project each initial day for a number of years, discard the transient behavior, and then plot the final results. In practice we have found that convergence to a characteristic seasonality occurs quite rapidly. The results from this procedure for the 4 weather data sets are shown in Fig. 2. Individual starting dates for both averaged temperature data sets converge to one of a few stable points (an attracting set), whereas both the specific simulations converge to an attracting cycle.

To investigate the effects of climate change, we modified the warmest habitat (warm-average) and coldest habitat (cold specific) data by adding 2.5°C to each hourly temperature. This procedure is a simple way of increasing annual mean temperature by 2.5°C, an increase within the range predicted by many gen-

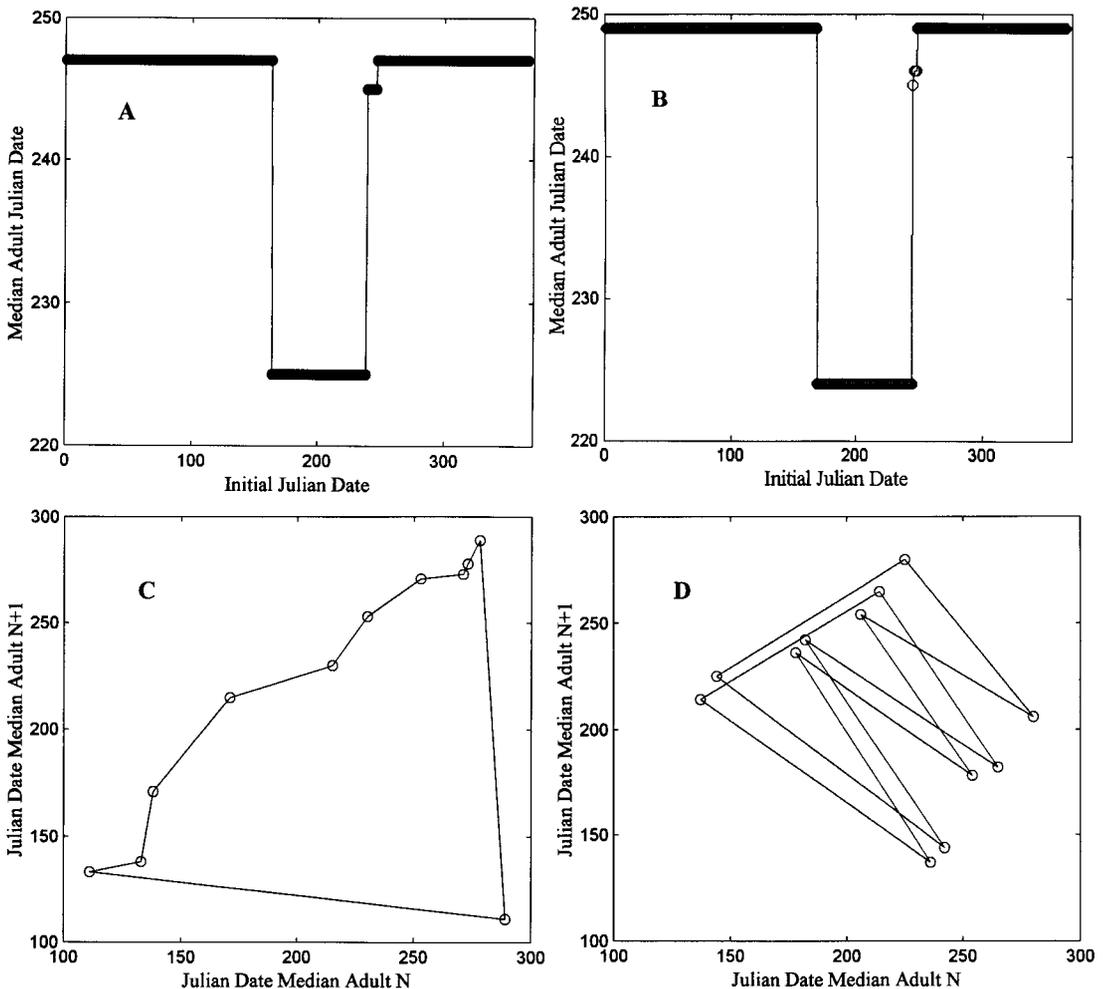


Fig. 2. Convergence trajectories for seasonality initiated from the maximally dispersed distribution of an egg oviposited on each day of the year. In the case of the two averaged temperature data sets, convergence is to a small [three dates for the warm averaged site (A), four dates for the cold averaged site (B)] set of attracting dates. In the case of both specific temperature data, convergence is to an attracting cycle [an 11 point cycle for the warm-specific site (C), and a complex 12 point cycle for the cold-specific site (D)].

eral circulation models for a CO₂ doubling scenario. The results of these 2 simulations are provided in Fig. 3. The additional thermal input shifted the cold specific dynamics from a cycle to an attracting set and the warm specific dynamics from an attracting set to an attracting cycle.

Discussion

Temperature Profiles. As illustrated in Fig. 1, the circannual temperature regime is complex, making direct ecological interpretation of this driving variable difficult. For example, answering the most basic question (i.e., Does the difference in temperature cycles shown in Fig. 1 have any ecological significance?) is essentially impossible without some quantitative tool (Amman 1985).

The annual degree-day accumulation for all data sets with the exception of the cold-specific data are above the threshold of 833 DD base 5.6 listed by Safranyik (1978) as the lower thermal threshold for univoltinism. The cold-specific data set was either just below (determined by integration) or just above (determined by summation) this threshold. Our model predicted generation times >1 yr for both of the specific data sets. This discrepancy is of indeterminate origin, but could arise from several sources. First, Safranyik's observations were made in Canada, so regional biotypes could have been selected for regional climates. A lower heat requirement for the more northerly Canadian population would be consistent with this hypothesis. Second, developmental rates, and subsequently phenology, depend not only on total thermal input, but are also sensitive to the seasonal

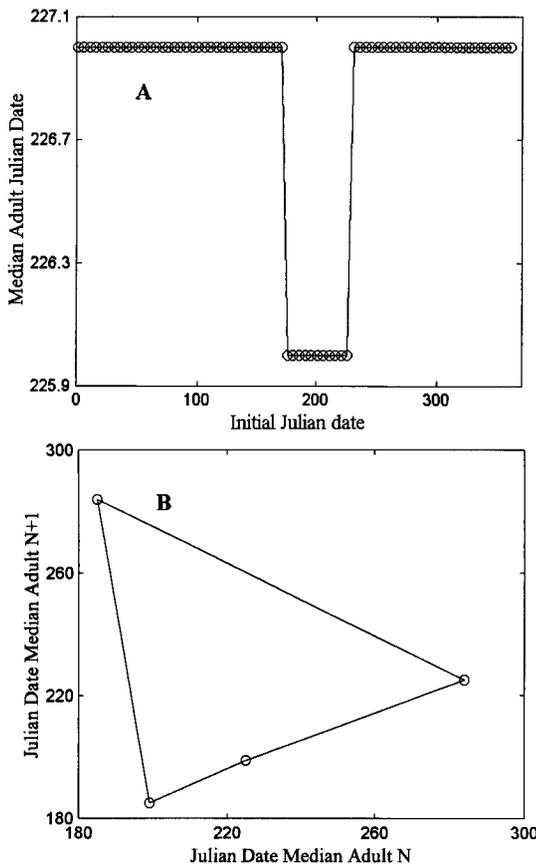


Fig. 3. Convergence trajectories for seasonality initiated from the maximally dispersed distribution of an egg oviposited on each day of the year for temperature data modified by adding 2.5°C to each hourly temperature. (A) The originally maladaptive dynamics of Fig. 2D were changed to the adaptive attracting set of 3A by warming the cold specific site temperatures. (B) The originally adaptive dynamics of the warm averaged site (Fig. 2A) were changed to a maladaptive cycle when temperatures were warmed.

pattern of this input. Seasonal phenology results from the interaction of two circle maps, one that describes progression through the various life stages, and the other that describes the pattern of seasonal temperatures. Complexities that arise from this interaction have been noted elsewhere (Amman 1985), but simply stated, it is possible to have annual temperature cycles with the same accumulated day degrees that result in quite different phenologies.

Characteristic Phenologies. As indicated in Fig. 2 A and B, the mountain pine beetle phenology model, which was based on independent data, resulted in a reasonable hypothesis of direct temperature control leading to an appropriate seasonality. The judgment of *reasonableness* is based on the following: (1) prediction of a strict univoltinism, in accordance with field observations from this part of the mountain pine beetle's geographic distribution; (2) predicting a seasonal occurrence of median adults that corresponds well

with the extensive field observations for this species in lodgepole pine stands of the Intermountain West (Reid 1962, Raffa and Berryman 1979, Amman and Cole 1983); (3) existence of a strong attraction for synchronous emergence. Phenological trajectories from a maximally dispersed (each day of the year) distribution of oviposition were strongly directed toward a compressed distribution of only 3 or 4 predicted median adult dates. These dates spanned a maximal range of 25 days (as compared with the initial 365 days). These results appear to be robust, spanning a range of conditions that represent both climatically favorable and unfavorable sites. Indeed, the characteristic phenology predicted from the 2 averaged temperature sites were quite similar. These results lead us to conclude that direct temperature control alone, without the necessity of an external stimulus other than temperature, is sufficient to explain the basic ecological requirement of an appropriate (adaptive) seasonality for mountain pine beetle.

There is a range of ovipositional dates that would result in a seasonally well timed median adult. Evolutionary theory, all other things being equal, would predict selection for the earliest emergence date that is consistent with avoiding freezing temperatures. In real world populations, where developmental rates are variable and to some extent genetically determined, selection pressure would further serve to synchronize the population by selecting for the earliest emergence date consistent with the regional climate. The earliest date of predicted median adult (13 August refer to Fig. 2 A and B) in both averaged data sets meet this basic seasonality criterion.

Newbold et al. (1994) discussed synchronization of emergence in their model of mayfly seasonality. They identify 2 factors that contribute to synchronous life histories. First is the effect of threshold temperatures in initiation of a developmental stage. In our model, the higher temperature thresholds of later larval instars allow early instars to "catch up" during the typically cool fall temperatures. This aspect of mountain pine beetle larval thermal development was fully described in Bentz et al. (1991). The 2nd factor identified by Newbold et al. (1994) is the effect of rising temperatures on developmental rates. If developmental rates are an increasing function of temperature, then clock time is compressed with respect to physiological time during warming periods (Taylor 1981). The compression of clock time occurs in our model during spring and summer when temperatures are in a domain of increasing developmental rates for all life stages. Therefore, both decreasing fall temperatures, and increasing spring temperatures can exert a synchronizing effect. Strong univoltinism for both averaged data results from the fact that individual initial conditions that reach median adult within one season subsequently iterate into a domain that projects to subsequent univoltinism.

Cold Year Temperature. A seasonality attractor also exists for both the cold-specific and the warm specific data sets, but instead of a set of attracting points, these attractors result in attracting cycles. These cycles,

Table 1. The 11 unique points on the attracting cycle shown in Fig. 2C

Initial day (N)	Median adult, days	Generation days	Generation time, years	Median adult date
171	580	409	1.12	3 Aug.
215	595	380	1.04	18 Aug.
230	618	388	1.06	10 Sept.
253	636	383	1.05	28 Sept.
271	638	367	1.01	30 Sept.
273	643	370	1.01	5 Oct.
278	654	376	1.03	16 Oct. ^a
289	841	552	1.51	21 April ^a
111	498	387	1.06	13 May ^b
133	503	370	1.01	18 May ^b
138	536	398	1.09	20 June

Emergence day (plotted in Fig. 1C reduced by modulo 365) are listed in total elapsed days from initial oviposition day.

^a Dates that are likely not survivable for adults or other freeze susceptible stages.

^b Emergence (in contrast to median adult) dates with high probability of subfreezing temperatures.

however, are not adaptive. There is, first of all, a breakdown in univoltinism, resulting in variable generation times (Tables 1 and 2). Although the resulting cycles are strongly attracting, some predicted median adult dates occur at inappropriate times. In addition, to the inappropriate seasonality, there is a breakdown in synchrony. Although it is true that any initial starting date will be attracted to the same cycle, they will converge to different points on the cycle (i.e., they are out of phase).

The breakdown in voltinism, seasonality, and synchrony leads to a climatic hypothesis for the geographic (elevational) distribution of mountain pine populations. The direct effect of cold temperatures on larval mortality has previously been reported (e.g., Amman 1973, Safranyik 1978, Amman and Cole 1983), although, recent experimental results (Bentz and Mullins 1999) show that the larval stages are more freeze

Table 2. The 12 unique points on the attracting cycle shown in Fig. 2D

Initial day (N)	Median adult, days	Generation, days	Generation time, years	Median adult date
265	912	647	1.77	1 July
182	607	425	1.16	30 Aug.
242	874	632	1.73	24 May ^a
144	590	446	1.22	26 Nov. ^b
225	645	420	1.15	7 Oct. ^b
280	936	656	1.79	25 July
206	619	413	1.13	11 Sept.
254	908	654	1.79	27 June
178	601	423	1.16	24 Aug.
236	867	613	1.73	17 May ^a
137	579	442	1.21	2 Aug.
214	630	416	1.14	22 Sept.

Emergence day (plotted in Fig. 1D reduced by modulo 365) are listed in total elapsed days from initial oviposition day.

^a Indicates emergence (in contrast to median adult) dates with high probability of subfreezing temperatures.

^b Dates that are likely not survivable for adults or other freeze susceptible stages.

Table 3. The 4 unique points on the attracting cycle shown in Fig. 3B

Initial day (N)	Median adult day	Generation days	Generation time, years	Median adult date
185	284	99	0.27	11 Oct.
284	590	306	0.83	13 Aug.
225	564	339	0.93	18 July
199	550	351	0.96	4 July

Emergence day (plotted in Fig. 3B reduced by modulo 365) are listed in total elapsed days from initial oviposition day.

resistant than previously appreciated. The deleterious effects of cold temperature that result in an inappropriate phenology provide an additional maladaptation that is independent of direct temperature mortality, but could none the less be lethal.

Climate Change Scenarios. As shown in Fig. 3A, increasing annual mean temperature by 2.5°C precipitated a change in system behavior of the cold-specific site from a maladaptive cycle to a strongly attracting set of fixed points. All 365 initial values converged to an attracting set with 2 points, differing by only 1 d. This attracting set satisfies the criteria of appropriate seasonality and synchrony. This result is not particularly surprising because the 2.5°C addition raised the annual mean temperature above the warm-average site, which we have already shown to be adaptive. What is interesting, however, is the clear demonstration that warming by a reasonable amount can transform a cold, inhospitable habitat to a benign, thermally favorable habitat. The implication is that global warming would result in a geographic shift northward, and also into previously marginal high elevation sites.

In the same sense that Fig. 3A demonstrates that warming can moderate an unfavorable thermal habitat, Fig. 3B indicates that increased warming is also capable of disrupting a favorable habitat. The shift from a set of adaptive attracting points to a maladaptive attracting cycle caused by warming is an interesting concept. Details of the resulting breakdown in seasonality are listed in Table 3.

The breakdown in seasonality shown in Table 3 is not as severe as indicated in Table 1 (i.e., all emergence dates are at survivable times during the year). However, the lack of synchrony could still be devastating to the essential mass attack strategy, particularly at low beetle population densities. The predicted decreased synchrony is consistent with a prolonged emergence period that has been observed in the southern distribution of mountain pine beetles (B.J.B. and Pat Shea, personal communication). Unlike cold temperature, it is unlikely that phloem maximum temperatures ever reach lethal levels. Patterson (1930) observed brood survival at prolonged temperatures in excess of 37°C. The asynchronous pattern resulting from warming of a favorable habitat provides a hypothesis for one factor limiting the southern distribution of mountain pine beetle, the observed distribution of which is well north of that for its *Pinus* host species. As populations progress south, interference

with voltinism and synchrony caused by increased thermal input results in a transition zone between univoltinism and bivoltinism. This transition zone could provide a substantial adaptive barrier to populations as they expand their southern distribution.

Direct temperature control of seasonality provides thermal plasticity that results in a system capable of regional/seasonal adaptation to varying environmental conditions (Bentz and Mullins 1999). Plasticity can be of both phenotypic and genetic origin, and has 2 important consequences. (1) The phenotypic responsiveness of mountain pine beetle to temperature makes it an ideal bio-indicator of climate change. Because this system integrates complex weather patterns that are predicted to result from climate change, monitoring for shifts in phenology could provide an early indication of changing climate. (2) Our model results indicate a reasonable phenotypic plasticity (the ability to maintain an appropriate seasonality in response to varying thermal regimes for fixed developmental rate parameters), although, the range of phenotypic adaptation is less than the distributional range for mountain pine beetles. This result implies that phenologically based population models developed for management or other specific applications may need to be parameterized on a regional basis.

Evaluation of Model Performance. The MATLAB model we developed is an efficient tool for assessing the qualitative characteristics of insect seasonality. The performance criterion for this model is 0.0075 s per simulation yr for solution of equation 2 after the table lookup of equation 1 has been completed. Solution of equation 1 for the eight life stages in the mountain pine beetle model requires 1.01 s for 2 yr of hourly temperature data. Setting up FOR loops to reinitialize simulations (a relatively inefficient process in MATLAB) and plotting results requires additional computer time. Even so, the 3,650 simulations required to investigate convergence properties for 1 of our data sets requires ≈ 15 min. CPU time, a significant savings over the 2.5 d that would be required using MPBMOD.

Conclusions. The reader is reminded that the purpose of our modeling exercise was to investigate the potential for direct temperature control of mountain pine beetle seasonality. The model was not intended to be a recreation of events as they occur in nature in that it lacks representation of mortality, and possible pupation and adult emergence thresholds, all of which could influence observed seasonality. However, given this caveat, several important qualitative conclusions follow.

(1) The MATLAB model we describe is an efficient empirical tool for investigating the dynamical properties of insect phenology.

(2) Strong, adaptive univoltinism is an emergent property of the mountain pine beetle model. We deem this highly unlikely to have occurred by pure chance. Thus, we conclude that direct control alone, without the requirement of an external stimulus other than temperature, is sufficient to explain the basic ecolog-

ical requirement of an appropriate (adaptive) seasonality for mountain pine beetle.

(3) The breakdown in adaptive phenology precipitated by both cooling and warming could provide a physiological explanation for the observed geographic and elevation distribution of this ecologically important species.

(4) All other things being equal, natural selection will favor increasing population growth rate. There are basically three ways to increase population growth rate: (1) decrease generation time, (2) increase fecundity, (3) decrease mortality. Our modeling results indicate that direct temperature control resulting in a strong adaptive phenology may provide an insurmountable barrier to selection for (1). Selection in climatically benign environments should, therefore, act to increase (2) and (3). Both of these latter two factors have been positively correlated with increased size, an observed characteristic that increases with decreasing latitudes for widely distributed species (Masaki 1973). This model prediction is consistent with empirical observations for mountain pine beetle (Bentz 1999).

(5) As a result, the integrative effect of biological systems combined with direct temperature control of seasonality, mountain pine beetle is an important indicator species for climate change. Dynamical properties of seasonality should be monitored in geographic regions of marginal thermal environments (e.g., high elevation pines, such as whitebark and limber pine) as a bio-indicator for climate change.

(6) For all 6 temperature sets examined (including the two generated from climate change scenarios), the qualitative behavior for any temperature cycle is uniquely determined by starting from any initial condition (ovipositional day). We suggest that this qualitative character is true for any realistic circannual temperature cycle. If this conjecture is true, it is not necessary to perform convergence experiments for every day in the year. Characterization of the global convergence properties may require checking only one or a few initial conditions.

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Appendix 1

The following MATLAB m-file was used to create the plots shown in Figs. 2 and 3. The file is currently set up to discard transience and plot only the last simulation year results. The phase plots for an attracting cycle are obtained by commenting out (a "%" character in MATLAB) the first x and y vectors and using the second x and y vectors. The names of appropriate temperature and parameter files need to be changed in the command that executes devrats.

```
% M-file Sim_controll;
figure;
hold;
step=1; % change to change step size;
count=0;
for i=1:step:365; % Set up to run a simulation for each
day in the year i;
```

```

count=count+1;
%
% change the temperature file to the desired file that
  has been loaded;
% remember to load the parameter "p" file;
%
[m_d_e_p_s] = devrats(ran_inf(:,3),p,i);% Change
  these names;
%
% the next two commands discard all transience and
  plot only the last simulation year;
%
x(count)=i;
y(count)=p_s(20,2);
% the next two commands plot last 13 simulation years
  - used to create the phase plots;
% of Fig. 2 (c) & (d) and 3(b);
%;
%x(1:13)=p_s(8:10,1);
%y(1:13)=p_s(8:10,2);
plot(x,y,'o-');
end

```

The m-file devrats is the actual simulation model.

```

function [med_day_emerg,phase_space] = devrats
  (x,p,da_start);
%;
% function [med_day_emerg,ndays] = devrats(tmp,p)
% program to compute solve for median days for com-
  pleting the six;
% life stages Logan & Amman for egg; Bentz, et al for
  ll - pupae; fitted;
% Stinner fct for general adult; and Ovipositional life
  stage from Logan et al.;
% (1995);
% temperatures are in array "tmp" that has 24*ndays
  rows;
% developmental rate parameters are in array p, where
  the ith row contain;
% the j parameters for the ith life stage;
% metamodel based on mpbmod;
%;
[m,n]=size(x);
ndays=fix(m/24);
y=reshape(x,24,ndays)';
%;
% compute the proportion of the life stage completed
  for each day in the;
%temperature data set for each life stage in the model
%;
dev_day(1,1:ndays)=(sum(alogan1(y-8,p(1,:),2)/24)');
dev_day(2,1:ndays)=(sum(blogan(y-5,p(2,:),2)/24)');
dev_day(3,1:ndays)=(sum(blogan(y-10,p(3,:),2)/24)');
dev_day(4,1:ndays)=(sum(alogan(y-15,p(4,:),2)/24)');
dev_day(5,1:ndays)=(sum(linear(y,p(5,:),2)/24)');
dev_day(6,1:ndays)=(sum(linear(y,p(6,:),2)/24)');
dev_day(7,1:ndays)=(sum(stnrat(y,p(7,:),2)/24)');
dev_day(8,1:ndays)=(sum(gallery_ln(y,p(8,:),2)/24)');
%;
% simulation loop starts here;

```

```

%;
nyrs=20; % set the number of simulation years here
med_day_emerg(1:nyrs,1:8)=NaN;
%;
% Begin computation of stage-specific developmental
  indices;
%;
for i=1:nyrs;
  test=cumsum(dev_day(1,da_start:ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,1)=(da_start)+fndlidx(test,1,1);
  test=cumsum(dev_day(2,med_day_emerg(i,1):
    ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,2)=med_day_emerg(i,1)
    + fndlidx(test,1,1);
  test=cumsum(dev_day(3,med_day_emerg(i,2):
    ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,3)=med_day_emerg(i,2)
    + fndlidx(test,1,1);
  test=cumsum(dev_day(4,med_day_emerg(i,3):
    ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,4)=med_day_emerg(i,3)
    + fndlidx(test,1,1);
  test=cumsum(dev_day(5,med_day_emerg(i,4):
    ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,5)=med_day_emerg(i,4)
    + fndlidx(test,1,1);
  test=cumsum(dev_day(6,med_day_emerg(i,5):
    ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,6)=med_day_emerg(i,5)
    + fndlidx(test,1,1);
  test=cumsum(dev_day(7,med_day_emerg(i,6):
    ndays));
  if(max(test)<1.0),break,end;
  med_day_emerg(i,7)=med_day_emerg(i,6)
    + fndlidx(test,1,1);
  test=cumsum(dev_day(8,med_day_emerg(i,7):
    ndays));
  if(max(test)<32.0),break,end;
  med_day_emerg(i,8)=med_day_emerg(i,7)
    + fndlidx(test,32,1);
  phase_space(i,1)=da_start;
  da_start=modulo(med_day_emerg(i,8),365); %
    modulo reduction
  phase_space(i,2)=med_day_emerg(i,8);
end;

```

The following m-files are utilities that are used by devrats. The individual m-files are separated by "#####." Utility files are included in the order that they are executed in devrats. All other functions are standard MATLAB functions.

```

function [y] = alogan(tmps,p);
% function [y] = alogan(tmps,p);
% this function takes as input the vector 'temps' of
  temperatures and returns;

```

```

% a vector y of the rate/temperature function
% 'alogan' value for each temperature in
% temps, for parameters p1=psi, p2=increase rate,
% p3=max temperature, p4=del t
% (high temp boundary)
% use:
% y=alogan(x,p)
%
z1=p(1)*(exp(p(2)*tmpls)-exp(p(2)*p(3)-(p(3)-
tmpls)/p(4)));
z2=z1>0; % filter for rates less than zero
y=z1.*z2;
#####
function [y] = blogan(tmpls,p)
%
% function [y] = alogan(tmpls,p)
% this function takes as input the vector 'temps' of
% temperatures and returns
% a vector y of the rate/temperature function 'alo
% gan' value for each temperature in
% temps, for parameters p1=psi, p2=increase rate,
% p3=max temperature, p4=del t
% (high temp boundary)
% use:
% y=blogan(x,p)
%
z1=1./(1+p(2).*exp(-p(3)*tmpls));
z2=exp(-(p(4)-tmpls)/p(5));
z3=p(1).*(z1-z2);
z4=z3>0; % filter for rates less than zero
y=z3.*z4;
#####
function [y] = linear(tmpls,p)
z1=p(2)*(tmpls-p(1));
z2=z1>0;
y=z1.*z2;
#####
function [y] = stnrat(tmpls,p)
% Stinners developmental rate curve
t=tmpls;
t(find(t>p(4)))=2*p(4)-t(find(t>p(4)));
y = p(1)./(1 + exp(p(2) + p(3) * t));
#####
function [y] = gallery_ln(tmpls,p)
% function [y] = gall_ln(tmpls,p)
% gallery length constructed as a function of temper
% ature for mpb - see Logan et al.
% IUFRO Hawaii Proceedings Logan, J. A., P. V. Bol-
% stad, B. J. Bentz, & D. L. Perkins.
% 1995. Assessing the effects of changing climate on
% mountain pine beetle dynamics.
% pp. 92-105 In Tinus, R. W. [ed.], Proceedings, In-
% terior west global climate workshop.
% USDA-Forest Service GTR-RM-262. 25-27 April
% 1995, Fort Collins, CO.
%
%;
% p(1) - P(3) are est parameters; p(4) is tau; p(5) is
% base Temperature;
t=tmpls-p(5);
i=find(t<0);
t(i)=0;
tau=t./p(4);
y = (p(1) * (exp(p(2).*t.^p(3)) - exp(-tau))) * 2.54;
#####
function indx = findlidx(x,v,s);
% index = findlindex(x,v,s);
%
% this function returns an index to vector x as follows:
% if s >= 0, then index is the smallest index s.t.
% x(index) >= v;
% if s <= 0, then index is the smallest index s.t.
% x(index) <= v;
%;
% see also: FIND, SORT;
%;
if (s>=0);
indx=min(find(x>=v));
else;
indx=max(find(x<=v));
end;
#####
function z = modulo(x,y);
%;
% z = modulo = (x,y);
% function to return the modulo of (x,y). Where z is
% the remainder after dividing;
% x by y;
%;
z = x-(floor(x/y)*y);

The parameter file that defines the developmental
rates for the mountain pine beetle model.

2.9800000e-002 1.4160000e-001 2.2514600e+001
3.1642000e+000 NaN
1.0189010e+000 7.2245790e+001 3.3933600e-001
2.4229400e+001 4.3073450e+000
1.0016100e+000 3.6704920e+001 3.7767600e-001
1.8335160e+001 3.9054210e+000
7.8989000e-002 8.5548000e-002 1.3049080e+001
1.5090730e+000 NaN
1.0933650e+001 1.0013000e-002 NaN NaN NaN
1.3099820e+001 2.2251000e-002 NaN NaN NaN
1.1911800e-001 9.3925957e+001 -5.277388e+000
2.4055651e+001 NaN
1.6900000e-001 1.9400000e-002 1.5400000e+000
8.0000000e-001 2.0000000e+000

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```