

Chapter 4, Part b

ANIMAL LIFE CYCLE MODELS

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INTRODUCTION

Maintaining an appropriate seasonality is a basic ecological requisite for all organisms. Critical life-cycle events must be keyed to the appropriate seasonal cycles, whether it be the wet-season/dry-season cycle of the tropics or the summer/winter cycle of temperate zones. The more pronounced the seasonal climatic signal, the stronger the requirement for an appropriate timing maintained through phenology. Although the importance of adaptive seasonal timing is no less for warm blooded than for poikilotherms (e.g. appropriately timed reproduction, hibernation), the primary application of phenology models has been for plants and cold-blooded animals.

The phenological habitat can conveniently be thought of as a hyperspace with temperature, moisture, nutrition, and photoperiod comprising the defining axes. The potential effect of moisture on phenology is expressed as a mortality differential, especially at extremes. Photoperiod is a consistent seasonal variable in the temperate zone that serves as an important environmental cue for initiation of critical events such as diapause (a physiological hibernation or aestivation state in insects). Diapause is a basic physiological process that typically serves to synchronize and reset the seasonal cycle of phenological events in face of desynchronizing variability in seasonal temperatures. Nutrition can affect phenology in the same way as moisture through mortality, or by altering developmental rates. It can also serve as an environmental cue for initiation of diapause.

Temperature is the strongest determinant of poikilotherm phenology, and is also the best understood. Thus, the focus of phenology modeling efforts has been to relate temperature to resulting phenological events. There is a large body of scientific literature relating the phenological responses of poikilotherms to temperature. Much of this knowledge pertains to insects or their close relatives. Our focus will, therefore, be on modeling seasonal life

cycles of insects. The underlying physiological mechanisms of response to temperature are similar enough that the methods we describe are applicable to all poikilotherms.

TEMPERATURE-DEPENDENT MODELS

Relating temperature to the development of insects, requires differentiating between *age* and *stage*. Although both are related to time, age is strictly chronological in nature, while stage is a developmental concept typically defined by distinct morphological characteristics often requiring a molt for transition from one stage to the next. Another time-related concept, *developmental rate*, is the temporal progression through an instar or stage and is dependent on temperature in a predictable fashion. Assuming that it is a constant function within a stage, the developmental rate, $r(T)$, at a constant temperature, T , is the inverse ($1/t$) of the time required to complete that life stage. For variable temperatures, $T(t)$, where t is time, we define a developmental index or *physiological age*, a , as,

$$\frac{d}{dt}a_j(t) = r[T(t)]; \quad a_j(t = t_{j-1}) = 0; \quad a_j(t) = \int_{t_{j-1}}^t r_j[T(t)] dt; \quad a_j(t = t_j) = 1 \quad [1]$$

Life stage j begins at t_{j-1} , which is the time of completion of the previous life stage (t_{j-1} as indicated by the initial condition of the differential equation above). Numerically, *developmental increments*, $\Delta a_j = r[T(t)]\Delta t$, during short time steps Δt are summed over time until $a_j = 1$, which indicates completion of life stage j and defines t_j , the time at the end of the life stage j .

These relationships underlie almost all models of insect phenology (see Logan & Powell 2001). Once the mathematical relationship between temperature, time, and physiological age is defined, there remains the issue of finding an appropriate functional relationship between temperature and the developmental rate, $r(T)$.

Developmental Rate Functions

The earliest functional form used to describe the relationship between temperature and rate of development was the linear or *day-degree* model, a concept that dates to the 1700s (Wang 1960), and has been extensively used to model both animal and plant phenology. Parameters in the day-degree model can be estimated from either field or laboratory data. Laboratory data typically consist of experimentally measured developmental rates over a range of fixed temperatures. Field estimates are obtained by assuming a

reasonable threshold temperature and then summing (integrating) temperature in excess of the threshold over time (often in days) until “heat units” accumulate to a specific total. Day-degree models often work well if the temperatures of ecological interest do not fall outside of the linear region of the organism’s thermal response (Fig. 1a). Their advantage is simplicity in estimating parameters and making phenological predictions. Their disadvantage is that they only constitute a more or less adequate approximation (Wang 1960).

The observation that developmental rates are nonlinear was made over 60 years ago, at least (Janisch 1932). It was not, however, until the mid 1970s that the use of nonlinear rate functions became widely practiced, mostly in response to the widespread availability of digital computers that provided methods for parameter estimation and convenient numerical solution of equation [1]. Stinner et al. 1975, Logan et al. 1976, and Sharpe &

DeMichele 1977 described nonlinear functions for insect temperature dependent developmental rates that have been widely applied since their introduction. This large body of literature supports the general shape of the developmental rate function as an exponential phase at low temperatures increasing to an optimum, and then a precipitous decline from the optimum temperature to the lethal thermal maximum (Fig. 1a). Parameter estimation for nonlinear developmental rate models is more complex than for linear based day-degree models. Procedures for estimating parameters of non-linear development rate functions have been automated for a reasonable suite of equations (Wagner et al. 1984, Logan 1988). A nonlinear rate model is required whenever simulations must cover temperatures over the full range of physiological activity. Life cycle phenomena that involve temperature extremes (diapause for example) also require nonlinear representation. The widely reported acceleration of development under the variable temperature regimes that occur in nature is the natural consequence of non-linearity (e.g., Tanigoshi and Logan 1979, Ruel & Ayres 1999). Given the availability of

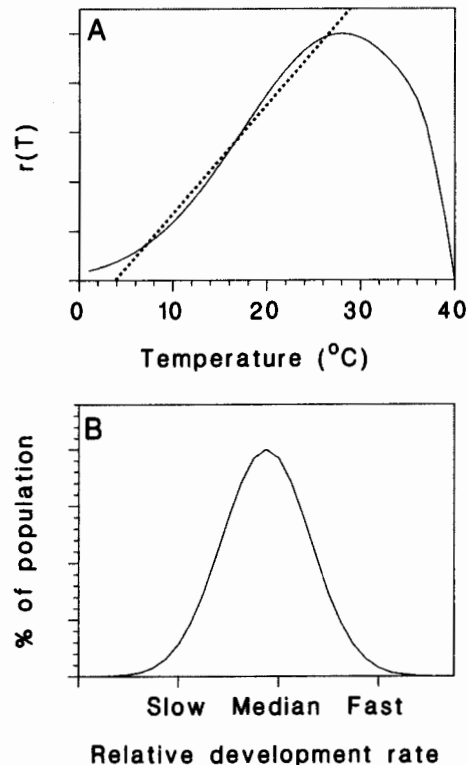


Figure 1. (A) Typical shape of poikilotherm thermal response (development rate, in days⁻¹). (B) Typical distribution of individual development rates relative to the median at a given temperature.

digital computers for both parameter estimation and simulation, there is little reason not to use nonlinear rate functions.

Modeling the Life Cycle

Once appropriate functional forms of $r(T)$ for each life stage have been established, phenology prediction becomes a question of solving equation [1] for the value of t_j for each life stage j (for a graphical description of modeling phenology with equation[1], see Logan & Powell 2001). Day-degree models are easily evaluated. For models with nonlinear rate curves, the easiest approach is to use numerical integration for direct solution of equation [1]. Procedures are available for automated construction and application of nonlinear rate based phenology models as well (e.g. Logan 1988).

Prediction of phenology and particularly the entire life cycle is best represented in mathematical terms as a circle map, relating the occurrence of critical phenological milestones in one generation to their occurrence in the next. A mathematical function describing this circle map can then be used for analyzing the stability characteristics of seasonality (Powell et al. 2000, Logan & Powell 2001; Régnière & Nealis 2002). Analysis of this function, the *G-function* in Logan & Powell (2001), has produced several interesting results. If conditions are sufficient for existence of an attracting date, then subsequent iterations on the annual cycle will be attracted to this date, even without a diapause or other physiological bio-fix mechanism. Not only will subsequent phenological cycles be attracted to this date, but also they will do so with at least exponential rapidity. This is an indication of the capability of insects to adapt to changing climatic conditions.

Including Developmental Variability

Ecological and biological phenomena often depend as much on variation in the population (Fig.1b) as on the average response. It is, therefore, often useful to include variability in developmental rates in phenology models. A common way of doing this is through time varying distributed delays, a technique borrowed from engineering (Forrester 1961; Manetsch 1976; Vansickle 1977). An advantage of distributed delays is availability of computational algorithms for implementation due to their wide application in engineering and other areas of applied mathematics. The major disadvantage is lack of flexibility in representing the distribution of developmental times.

Cohort models have often been used to include variability in developmental rates (Curry et al. 1978). This modeling approach uses computed physiological age as the independent variable for cumulative

probability density function of stage completion. The approach assumes that the normalized distribution of developmental rates is invariant with temperature. Once this assumption is made, simulation is a simple matter of computing physiological age of all cohorts (a cohort is typically defined as the individuals that entered a life stage during one time step of the model) that comprise a life stage. Development and implementation of these types of models has been automated (Logan 1988). The advantage of cohort approaches to modeling phenology is flexibility in choice of distribution models. The primary disadvantage is the “same shape” assumption, which is questionable at temperature extremes.

With the relentless advance in computing power, it is becoming more practical to simulate population processes through sub-populations (Régnière 1984) or individual based models. In the latter approach, a sample population is drawn from an observed or assumed distribution of developmental rates (Fig. 1b). Simulation is performed by solving equation [1] for each individual in the population. The advantage of individual based models is complete flexibility in selection of both developmental rate functions and probability density distribution. The major disadvantage is computational overhead. Depending on the type of application, this method may be too computationally intensive. However, object-oriented programming techniques have greatly enhanced the efficiency and usefulness of individual-based phenology modeling (e.g., Cooke & Régnière 1996).

MODELING LANDSCAPE INFLUENCES

One of the areas of central interest in animal ecology is the influence of landscapes on the outcome of ecological processes as environmental conditions, plant communities, and movement influence them (Haila 2002; McGarigal & Cushman 2002). The ability to model these influences at the landscape level is a key to improving our predictive understanding of these outcomes so as to improve area-wide management of pests, resources and ecosystems (Boutin & Hébert 2002; Ryszkowski 2002). In the ecology of poikilotherms, landscapes play a key role in determining patterns of abundance through their influence on local climate (Chen et al. 1999). A system called BioSIM[©] was developed by Régnière et al. (1996) to perform most of the functions described below.

Main Influences of Landscape on Climate

Whiteman (2000) lists four factors that determine local climate over a given landscape: latitude, altitude above sea level, continentality (distance from the sea) and exposure to regional circulation (winds and ocean currents). Other factors that can also influence local climate are cold-air drainage and terrain shading, both particularly important in steep landscapes (Bolstad et al. 1998).

Gas physics, moisture content and solar radiation explain much of the effects of latitude and elevation on air temperature over a landscape. Usually, these influences are modeled with thermal gradients. A dry (unsaturated)

parcel of air cools by 0.98°C per 100 m elevation (the adiabatic lapse rate). In addition, air temperature drops by about 1°C per degree of latitude away from the equator. Actual thermal gradients are usually smaller than the adiabatic lapse rate, vary with location, time of year, and even time of day (Régnière and Bolstad 1994), in large part in response to the amount of moisture in the air, its general temperature, air circulation patterns and the proximity of large water bodies. For example, minimum (nighttime) and maximum (daytime) air temperature elevation gradients on the Pacific coast of British Columbia are very different from each other. Minimum temperature gradients average less than -0.5°C per 100 m. Maximum temperature gradients are actually inverted (positive) in summer months as a result of cold-water maritime influence (Fig. 2a). Latitudinal gradients in the area are strongly patterned seasonally, with temperatures cooling down northward in winter, and actually warming northward in summer (Fig. 2b), once again due to the presence of cold waters in the southern part of the area. Longitudinal gradients are also strongly patterned over the year (Fig. 2c).

Several methods have been devised to interpolate climatic variables from a number of punctual data sources over a surrounding landscape. Two are of particular interest because of their relative simplicity and because of the

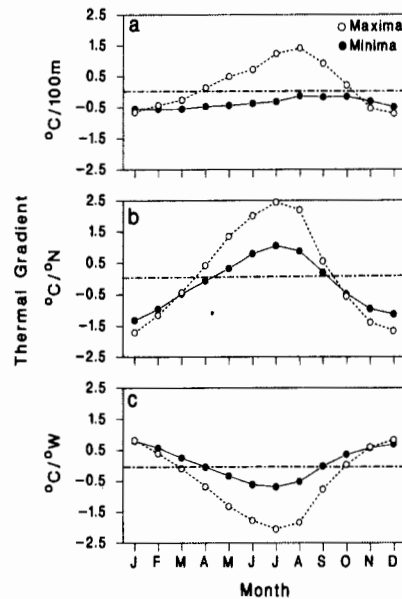


Figure 2. Monthly thermal gradients from 1961 to 1990 averages for Vancouver Island and the Pacific coast of British Columbia (Canada). (a) elevation, (b) latitudinal and (c) longitudinal gradients.

general availability of their algorithms: GIDS (for Gradients with Inverse Distance Squared weighting; Nalder & Wein 1998) and ANUSPLIN (thin-plate smoothing splines; Hutchinson 1991). While their performance is very similar (Price et al. 2000), GIDS is most attractive because of its simplicity. It uses multiple linear regression fitted to data from a number (we have used 20) of nearby weather stations:

$$Y = a + m_E E + m_N N + m_W W \quad [2]$$

where Y is a climate value (e.g., minimum air temperature), E is elevation, N is latitude and W is longitude of the region's weather stations; a is an intercept constant, and m_E , m_N and m_W are regional thermal gradients for elevation, latitude and longitude. These are applied to differences in latitude (ΔN), longitude (ΔW) and elevation (ΔE) between the unsampled locations and a number (we have used 4) of the nearest weather stations.

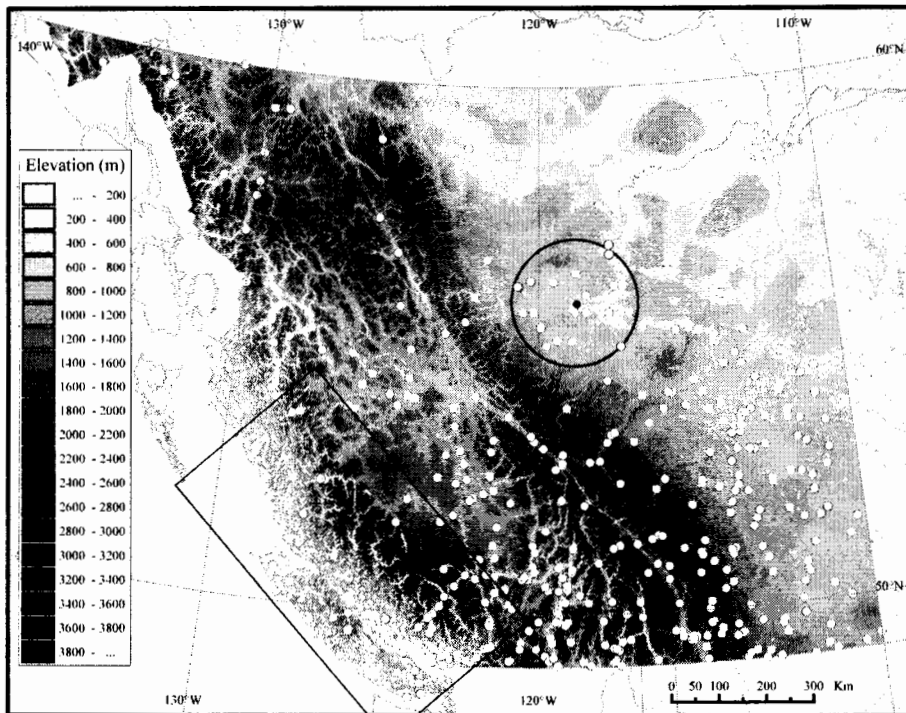


Figure 3. Digital elevation model of British Columbia and Alberta (Canada). Climate information for unsampled locations (●) can be obtained simply by the GIDS method (Nalder and Wein 1998) where data from several nearby weather stations (○) are used to estimate regional thermal gradients by multiple linear regression. These gradients are then applied to differences in latitude, longitude and elevation between station data and unsampled location (an inverse distance-squared weighted average). The rectangular area contains the weather stations used to estimate thermal gradients in Fig. 2.

The inverse of the squared distances ($1/d^2$) between these n nearest stations and unsampled locations are used as weights in the estimation of the climate datum (Y_u):

$$Y_u = \frac{\sum_{i=1}^n \frac{1}{d_i^2} (Y_i + m_E \Delta E_i + m_N \Delta N_i + m_W \Delta W_i)}{\sum_{i=1}^n \frac{1}{d_i^2}} \quad [3]$$

This process (Fig. 3) can be applied equally well to monthly climate statistics (normals) or to daily records to obtain air temperature and precipitation information for any number of unsampled points across a landscape. Difficulties in application of this methodology sometimes arise when weather stations are exceedingly sparse or do not cover the range of elevations found in the landscape (multiple regression models are notoriously poor at extrapolation). For that reason, our implementation of the GIDS algorithm doubles, then triples, the number of stations used to estimate gradients whenever the elevation of the unsampled location is outside of the range $\pm 10\%$ found among the set of nearby stations.

Daily Weather Generators

Daily weather generators play an important role in the investigation of climatic influences on animal ecology, because of the cumulative nature of daily or even hourly conditions. This level of detail is especially important in understanding the ecology of fast-developing cold-blooded animals, such as insects. As discussed in earlier sections of this chapter, thermal responses are strongly non-linear even when described by degree-day approximations. Thus, average outcomes cannot be obtained from average inputs. Thirty days of monthly average temperature does not have the same effect as 30 days of variable temperature with the same average. This has been called the Kaufmann effect (Worner 1992).

When general questions concerning past climate are asked, answers can often be obtained by providing models with actual past weather records. However, such an approach has several limitations. First, past weather records usually cover a limited period at any given location (especially in North America). Second, it is never clear just how “general” a conclusion actually is about a given ecological process because of the limited amount of historical data available, especially in view of the extreme variability of weather conditions.

Daily weather generation provides a general approach that can be applied equally well to past, present and future (climate-changed) conditions.

Several daily weather generators have been developed (Richardson 1981; Richardson & Wright 1984; Racsko et al. 1991; Hutchinson 1995; Wilks 1999), but many require considerable amounts of input information and often must be re-parameterized for application in specific geographical areas. Régnière & Bolstad (1994) developed a generally-applicable algorithm (TempGen) for simulation of daily minimum and maximum air temperature using monthly normals (long-term average and extreme minimum and maximum temperatures). This generator is being expanded to generate realistic daily rainfall and solar radiation as well, and to mimic natural variation in mean monthly temperature and precipitation to simulate extreme events such as drought, untimely frost, heat waves, etc. It is also being validated for application in North America and Europe (unpublished).

Because TempGen uses monthly averages as input, it is quite well suited to accept the climate-change scenarios generated by Global Circulation Models (two examples that have become widely used are the CGCM1 model developed by the Canadian Centre for Climate Modeling and Analysis, and another by the Hadley Center for Climate Prediction and Research). Output from TempGen, based on climate-changed normals, can therefore be used readily to simulate the impact of global warming on ecological processes modeled from daily climate inputs.

Spatial Interpolation Methodology

Running simulation models of animal development that use daily weather inputs can be demanding even for relatively fast computers. This means that it may be prohibitively time consuming to produce model output for each unit (pixel, or raster) of a landscape (output map), except with the simplest of degree-day models (e.g. Russo et al. 1993). A solution is to run models for a relatively small number (a few hundred) of randomly located points across a landscape, and to use a spatial interpolation method to estimate model output at other locations on the landscape. This approach was first proposed by Schaub et al. (1995), who used of a linear regression between elevation and phenological target event (which they called a t-function) to transform a digital terrain model of the landscape algebraically into a phenology map. Régnière (1996) expanded this t-function concept from a simple regression with elevation to a spatial regression using latitude, longitude, elevation, slope and aspect, their squares and interactions as predictors.

Régnière & Sharov (1999) used universal kriging with elevation as an external drift variable as an interpolation method (see Isaaks & Srivastava 1989 for methodological details). Although general rules are difficult to provide, it has been our experience that spatial regression does best over smaller and steep landscapes, where elevation, slope and aspect are the main determinant of climatic variation; over larger areas, or where topography is

less pronounced, kriging often does somewhat better (Gignac 2000). Other interpolation techniques exist, for example the GIDS method described earlier (which is a local-regression technique) or inverse-distance weighted averaging.

The choice of the most appropriate interpolation method can be made on the basis of cross-validation. This procedure consists of successively removing and replacing the known model output values at simulation points, estimating them by the chosen interpolation method and comparing the two sets (model output and the interpolated values). Simple coefficients of determination can be calculated to provide an objective comparison criterion between the interpolation methods tested (Fig. 4). In this example from spruce budworm (see below) the best interpolation method is spatial regression ($R^2 = 0.812$).

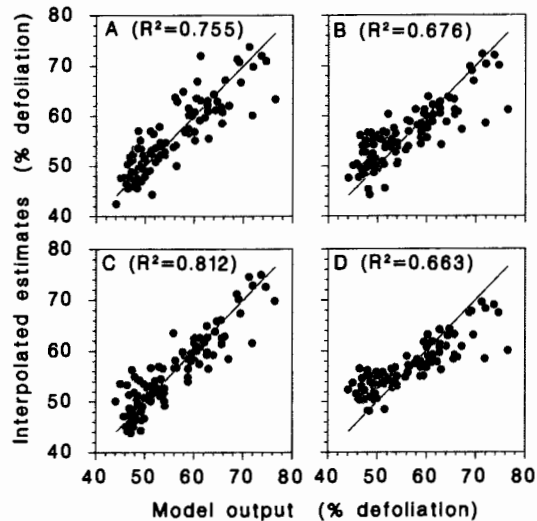


Figure 4. Cross-validation of defoliation by spruce budworm as predicted by Cooke's model and estimated by four spatial interpolation methods. (A) universal kriging; (B) GIDS; (C) spatial regression; and (D) inverse-distance squared weighted average. Lines are the equality diagonal.

EXAMPLES FROM ENTOMOLOGY

The Spruce Budworm

The spruce budworm, *Choristoneura fumiferana* (Clem.) is a tortricid moth whose larvae defoliate conifer trees (firs and spruces of the *Abies* and *Picea* genera) of northeastern North America on a somewhat regular cycle of 30-40 year (Royama 1984). It is an insect with obligate larval winter diapause, which means that by winter's end the entire population is synchronized in the early stages of post-diapause development; spring emergence of larvae occurs within a week, two at the most, as soon as sufficient development-inducing warmth has occurred. Cooke & Régnière (1996) developed an object-oriented, individual-based model to simulate interactions between spruce budworm, host trees, and the bacterium *Bacillus*

thuringiensis (*B.t.*) used as a bio-pesticide. The resulting so-called Cooke's model has been extensively validated (Régnière & Cooke 1998).

Cooke's model can be used as a landscape-level pest management tool to assist in optimizing the delivery of pest management operations such as sampling, pheromone trap deployment, and pesticide applications. The efficacy of aerial sprays of *B.t.* is non-linearly dependent on the stage of development of the target insect. Obviously, a pesticide application made prior to emergence of larvae, before the onset of feeding, will not be efficacious. An application made too late, after much of the feeding damage has been done, may kill insects but cannot protect foliage that has already been consumed. Thus, there is an optimal timing of applications that is based on topography, climate, insect thermal responses, the feeding ecology of the target stages and their specific sensitivity to the pesticide. Over complex terrain, spruce budworm development can cover a wide range (Plate X₁). The non-linear nature of the influence of timing on *B.t.* efficacy is apparent from the output of Cooke's model (Plate X₁): applications that are made too early (when the insect is still overwintering and has just started feeding) are the least efficacious as predicted in the mountains to the north and to the southeast of Quebec City. The most efficacious treatments occur when the insect is in instars 3 and 4. Treatments applied too late, past the 4th instar, are less efficacious as seen in the low-elevation area to the south and west of Trois-Rivières. This makes adequate timing of control operations using *B.t.* against spruce budworm quite critical to their success in protecting conifer foliage.

The Gypsy Moth

The gypsy moth, *Lymantria dispar* (L.) is a lymantriid that was accidentally introduced in eastern North America in 1869, and has spread gradually to the north, west and south since (Liebhold 1992). It is a periodic pest of deciduous trees, especially oaks (*Quercus*), maples (*Acer*), birches (*Betula*) and poplars (*Populus*) (Montgommery 1990). Hypotheses about the determinants of its rate of spread and eventual range on the continent, especially to the north, have focused on egg mortality due to low winter temperatures, or on forest susceptibility (Sharov et al. 1999). Limitations that the insect will encounter in establishing to the west and south of its current distribution are less well understood (e.g., Allen et al. 1993).

A detailed model of gypsy moth phenology was assembled by Régnière & Sharov (1998) from components found in the literature for the various life stages. The egg hatch component of this model was replaced by the detailed model of gypsy moth egg diapause built by Gray et al. (2001). The resulting model can simulate the entire life cycle of the insect through

successive generations in any climate. It was first used in the context of timing of an eradication program in British Columbia, Canada, in 2000 (Nealis et al. 2001).

Régnière and Nealis (in press) used the model to determine the areas of southern British Columbia that were most likely to support establishment of this exotic insect, on the basis of local climate. This analysis was based on whether or not the model predicted a biologically feasible life cycle for the insect in a given location under normal climatic conditions. If peak oviposition was predicted to occur no later than the end of October (a time when temperatures are too cold for eggs to enter diapause successfully) for 20 successive generations, the gypsy moth was presumed to have the potential of establishing there. This analysis is mathematically identical to the G-function developed by Logan & Powell (2001).

The same approach was used to produce a map of the probability of establishment of gypsy moth throughout the North American continent north of Mexico. A series of 27,360 simulation points was located randomly across the continent. Twenty-generation model runs were made for each point using daily weather data generated from local normals (using the GIDS local gradient method described earlier). For each model run, the outcome was rated as 0 (seasonality did not remain viable for 20 generations) or 1 (seasonality did remain viable). Each run was replicated 30 times (30 stochastically different daily weather traces), and the average outcome for each point was used as an estimate of the probability of gypsy moth establishment at that location:

$$P_i = \frac{1}{n+2} \left(1 + \sum_{j=1}^n p_{ij} \right) \quad [4]$$

where p_{ij} is the simulation outcome for point i and replicate j , $n = 30$ is the number of replicates and $0.02 \leq P_i \leq 0.98$. The resulting probability table was transformed to a logit scale for linearization:

$$g(P) = \ln \left[\frac{P}{1-P} \right] \quad [5]$$

and was then interpolated spatially by universal kriging using elevation as a drift variable, over a digital elevation model of North America at 30 arc second (≈ 1 km) resolution. The resulting map was back transformed to a probability scale by inverting equation [5] (Plate X₂).

The Mountain Pine Beetle

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a bark beetle (Coleoptera: Scolytidae) that has a large impact on ponderosa and lodgepole pine forests throughout western North America all the way from northern Mexico to central British Columbia (Logan & Powell 2001). There are two critical factors determining the ability of mountain pine beetle to overcome the defenses of its host tree to kill it and successfully reproduce: adequate seasonal timing and simultaneous attack by large numbers of beetles.

Thus, an adaptive seasonality for this insect implies that critical events in its life cycle be timed adequately, and that the development of the population not be so spread-out (variable) that large numbers of adults are not available for synchronous attack within a given summer. In most insects, winter diapause serves to halt development during the cold season and maintain the population in the early stages of post-diapause until temperature warms up in the spring, a process that resets the biological calendar and synchronizes the entire population. In the mountain pine beetle, however, there is no evidence of diapause in any life stage. In this species, seasonality seems entirely determined by the seasonal patterns of weather (Logan & Bentz 1999). Direct control of the insect's seasonality by weather patterns is intriguing ecologically and evolutionarily. It would seem that very complex spatial and temporal patterns of abundance could result from the detail of regional, even local annual temperature fluctuations.

A detailed phenology model is an ideal tool to address this type of question. Such a model is available for mountain pine beetle (Bentz et al. 1991; citations in Logan & Powell 2001). It is a distributed, non-linear description of the thermal responses of all stages of the insect's life cycle. Logan & Bentz (1999), Powell et al. (2000) and Logan & Powell (2001) studied the model's behavior and provided insight as to how temperature regimes alone could synchronize an insect population without recourse to diapause. There are three basic conditions for the seasonality of mountain pine beetle to be adaptive under a given annual temperature regime (as depicted by this phenology model): it must be univoltine, oviposition dates from generation to generation must converge to a near-constant time of year and this date must fall between biologically realistic bounds (early July to late August).

We generated maps depicting the likelihood of mountain pine beetle establishment and thriving, on the basis of the probability of it achieving adaptive seasonality as defined by the three criteria above. We applied climate change scenarios, defined by deviations in monthly mean minimum and maximum air temperature, to normals used by BioSIM[®]. These scenarios were obtained from the Canadian Centre for Climate Modeling and Analysis (<http://www.cccma.bc.ec.gc.ca/>), gridded at finer spatial resolution

(<http://www.cics.uvic.ca/scenarios/index.cgi?Scenarios>). Climate-changed normals (30-year averages) were calculated at 10 year intervals from the period 1971-2000 to 2041-2070. Actual normals were used for the 4 decades 1931-1960, 1941-1970, 1951-1980 and 1961-1990. Simulations (20 successive generations) were run for 500 randomly-located points in British Columbia and Alberta (Fig. 3), and each simulation was replicated 30 times for each set of normals. The logistic transformation (equations [4] and [5]) was used prior to applying universal kriging (with elevation as drift variable) to the resulting probability of adaptive seasonality, and the resulting maps were back-transformed to a regular probability (inverting equation [5]).

The resulting series of probability maps covers a 120-year time span (Plate X₃). The model predicts a gradual northward shift of the insect's most suitable range in British Columbia and Alberta. It also predicts a gradual restriction towards higher elevations as the climate of the region warms, disrupting the univoltinism requirement for adaptive seasonality in mountain pine beetle.

Currently, mountain pine beetle thrives in south and central British Columbia, and in the Cypress Hills area of southeastern Alberta. It is confined there by prairies and the high elevations of the Canadian Rocky Mountains. The northern part of Alberta is forested by jack pine, *Pinus banksiana*, a species that is only now coming in contact with mountain pine beetle in the mountain passes between central BC and Alberta (Logan & Powell 2001; personal communication, A. Carroll, Canadian Forest Service, Victoria, BC). However, it seems quite likely that the mountain pine beetle can spill over the natural barrier of the high mountains, given the increasing suitability of northern latitude and higher elevations as global warming proceeds.

CONCLUSIONS

The development of phenology modeling methodologies in the field of animal ecology has tended to precede somewhat that of computing technology in the past 30 years, since the introduction of nonlinear and distributed models of poikilotherm thermal responses. These models are becoming increasingly sophisticated, detailed and accurate, and the study of their behavior is teaching us about the evolution of seasonality and the effects of temperature on the distribution and population stability of poikilotherms. It is also becoming increasingly feasible to investigate the outcomes of phenological processes through models that make predictions over large, climatically and topographically complex areas.

These technologies allow us to use landscape-wide phenological projections in the conduct of area-wide Integrated Pest Management activities. They also provide us with the ability to study and better understand the ecology and distribution of indigenous species based on comparison of observations with model predictions. We can also use these tools to analyze

the probable reactions of these indigenous species to changing environments, most importantly climate change but also changes in the distribution of host plants resulting from human activity. Finally, these tools can be used to predict the probable distribution and thriving of invasive species, such as gypsy moth, as soon as we gain sufficiently detailed knowledge of their thermal responses.

Using Geographical Information Systems technology, it is also becoming relatively simple to merge the outcome of our detailed understanding of developmental processes with other, geographically critical information such as the distribution of susceptible plants, soils, water, as well as insect or disease survey data. This convergence of information constitutes the basis for investigation of more complex ecological issues that are always related to seasonality and phenology, but not always directly or simply.

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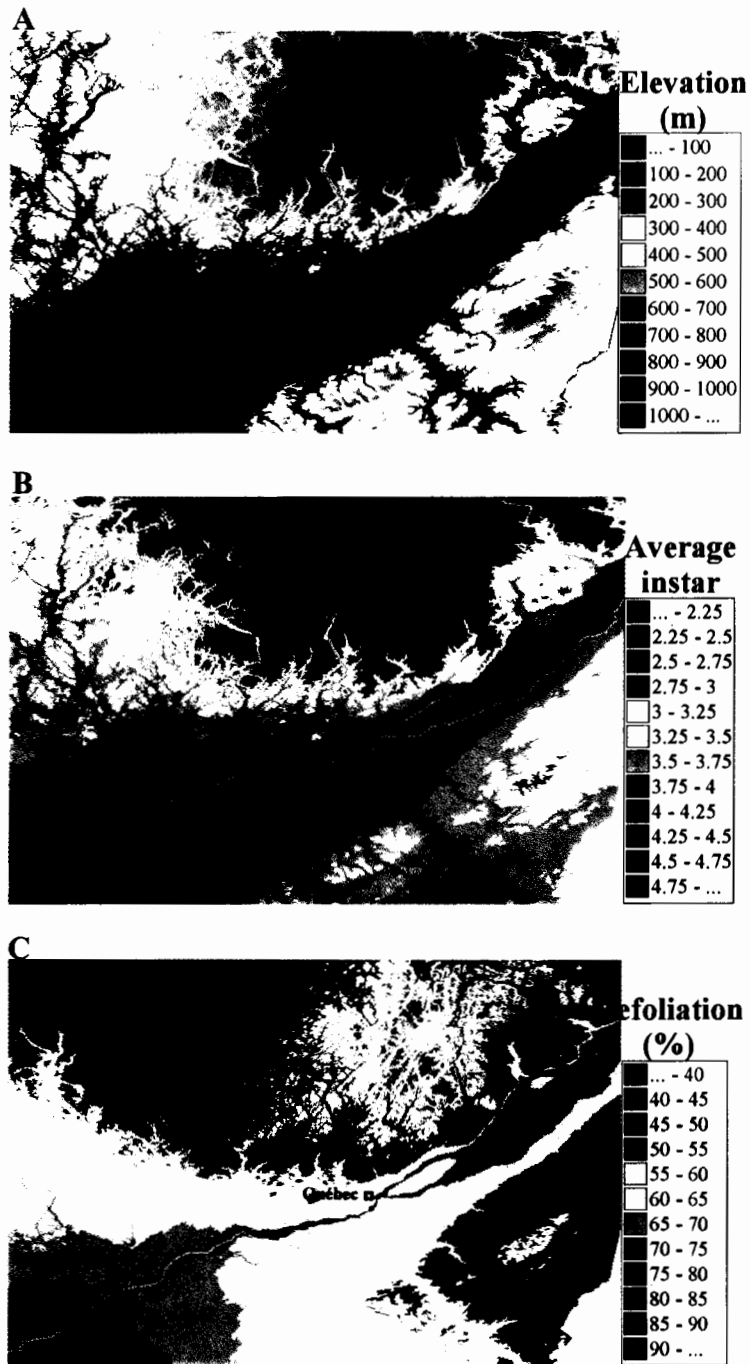


Plate X₁. (A) Digital elevation model of a region of Quebec, Canada, between 46°N, 70°W and 48°N, 73°W). (B) Phenology of spruce budworm (average instar in populations) on 1 June, based on 1961-1990 temperature normals. (C) Defoliation (%) expected after a double application of high-potency *B.t.* (60 BIU per ha) on 1 and 8 June.



Plate X₂. Probability of gypsy moth establishment in North America (north of Mexico) based on its ability to achieve an adaptive seasonality.

Plate X₃. Series of maps depicting the probability of Mountain pine beetle achieving an adaptive seasonality in British Columbia and Alberta, Canada, on the basis of daily temperature inputs generated from 30-year normals at 10-year intervals from 1931-1960 to 2041-2070