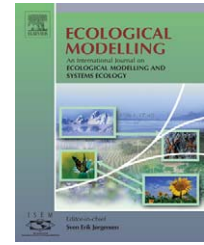


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Temperature-dependent phenology and predation in arthropod systems

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ABSTRACT

A central issue in ecology is to determine how environmental variations associated with global climate change, especially changing temperatures, affect trophic interactions in various ecosystems. This paper develops a temperature-dependent, stage-based, discrete, cohort model of the population dynamics of an insect pest under pressure from a predator. Guided by experimental data, the model is applied specifically to predation of grasshoppers by rangeland lycosid spiders. The development rate of insect arthropods is strongly affected by temperature, and these temperature-dependent phenological effects couple with shifts in the daily activity periods for both prey and predator, thereby increasing or decreasing opportunities for interaction. The model addresses these effects quantitatively by introducing a temperature-dependent, joint-activity factor that enters the predator's functional response. The model also includes a prey mortality rate that is temperature-dependent through the prey development rate. The model is parameterized using field and experimental data for spiders and grasshoppers. We investigate the effect of the solar power index (sunlight), mean temperature, and temperature variation, as measured by amplitude, on the developmental times and survivorship both with, and without, predation. We conclude that increasing variation in temperature results in a stronger relative effect on survivorship due to predation.

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1. Introduction

An important issue in ecological theory is to understand how increased or reduced temperature levels associated with global climate change will affect ecosystems (Walther et al., 2002), and in particular, trophic interactions (Kareiva et al., 1993; Joern et al., 2005). See Burns (2000) for a bibliography through the year 2000. It is especially important in the case of exothermic interactions to understand, assess, and predict when those interactions will become out of balance. In this paper we address this issue in the context of grasshoppers-spider interactions in grassland ecosystems. We develop a discrete dynamical model of an arthropod predator–prey interaction

that involves temperature effects. Precisely, a rational mechanism is proposed to integrate temperature-mitigated developmental and activity cycles in predator–prey models, filtered through the effects of a Holling type II response. The model has general elements that may apply to other trophic interactions.

Both discrete and continuous predator–prey models have formed a fundamental part of ecological theory since the work of Lotka and Volterra in the 1920s (e.g., see Murdoch et al., 2003, for a comprehensive introduction to consumer-resource dynamics and for extensive references, and Hassell, 1978, for specific arthropod dynamics). However, very few models have included explicit, mechanistic effects of temperature on the

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interactions (e.g., see Mack and Smilowitz, 1982; Gilioli et al., 2005). Yet, temperature levels can strongly affect the phenology of both predator the prey, as well as their activity times. Shifts in either the phenologies, emergence times, or activity periods can change the timing of the interactions and delay or magnify predation events. These kinds of effects are particularly critical for interaction of insect pests and their predators (Morales-Ramos et al., 1996; Xia et al., 1999a,b; Rochat and Gutierrez, 2001; Drechsler and Settele, 2001; Thomas and Blandford, 2003; Xia et al., 2003; Bianchi and van der Werf, 2004). Including temperature variation in many the existing models could alter the results and conclusions.

Generally, the speed of metabolism in poikilothermic organisms varies with temperature. This dictates their development rates (Gilbert and Ragworth, 1996; Gillooly et al., 2002), which are strongly nonlinear functions of temperature. Low temperatures slow development and increase the length of periods that the insects are in their various life stages. This can intensify stage-based predation. High temperatures speed development and can cause earlier emergence from the egg stage and a more rapid progression through the nymphal or other stages, giving adults increased periods of reproduction and escape from predation that often accompanies nymphal stages. Similar effects can be experienced by the predator. Further, temperature variations can effect daily activity periods, causing either the predator or prey to be more, or less, active. Therefore, predator search times can be strongly affected by temperature levels.

In the present model we only consider how temperature affects prey development and joint activity as they influence predation risk. We ignore other temperature effects. For example, for insect herbivores, food quality and digestion also vary as CO₂ increases; C:N ratios in plants are expected to increase, affecting both consumption and digestion rate (Ayers, 1993; Harrison and Fewell, 1995; Yang and Joern, 1994a,b). Therefore, when coupled with increased atmospheric CO₂ levels, temperature changes can have substantial eco-physiological effects (Ritchie, 1996; Newman, 2003). Decreased or strong variations in the daily temperature amplitude may mean that they cannot meet nutritional needs, leading to higher mortality. On the other hand, increased temperature could mitigate the effects of low food quality (Wolesensky et al., 2005; Wolesensky and Logan, in press-a,i; Logan et al., in press). These temperature–food quality–consumption interactions, which could certainly have major effects insect populations, are not discussed in this communication.

It is unlikely that any model will be able to predict populations with a high degree of accuracy. Rather, our goal is to examine qualitative changes that might occur when temperature is varied from a set of baseline values. In the model we consider a single prey cohort, hatched on the same day. The rate that each individual progresses through its nymphal period, as measured in degree-days per day, is temperature-dependent. The prey population density on a given day is governed by a difference equation (discrete model) that includes a natural mortality rate and a predation rate, both including temperature dependence. No effort in the model is made to resolve predator population dynamics. We assume the predator density is an input determined, for example, from field estimates. The natural mortality rate of the insect population

depends upon the instar, which is temperature-dependent through the development rate. The predation rate, which is a modified Holling type II functional response, is temperature-dependent through the total time available for the predator to search, capture, and handle the prey. The model is metered in the sense that information is updated each day by calculating hourly effects. Predation events occur on an hourly basis, depending upon the micro-habitat temperature. Spatial effects are not included in this model, nor is environmental or demographic stochasticity. With any model, obtaining accurate parameter values from data collected on experimental studies on real populations can be difficult. We take the view that our model is a tool both for expressing our ideas as to what factors affect population changes, and for deducing the effects of those factors alone.

In the last section we apply the model to estimate the magnitudes of natural mortality and spider predation on a grasshopper population. The model is parameterized using field and experimental data. With the model we investigate the effect of solar power index (incident sunlight), mean temperature, and temperature variation on the developmental times and survivorship both with, and without, predation. It is concluded that increasing variation in temperature results in a stronger reduction in survivorship due to predation. At one extreme (lower temperatures, higher daily amplitude variations, and lower sunlight), spider predation plays a more significant role in mortality than in the other extreme (higher temperatures, smaller amplitudes, and ample sunlight), where predation is less significant. The theory and calculations also confirm ecologist's belief that spider predation plays a lesser role in controlling populations than climate changes driving development and phenology. A similar approach may be applicable to other taxonomic, trophic interactions.

2. Model development

The model is a deterministic, discrete time model of prey dynamics, where H_n is the prey density on day n , measured in insects per m². The goal is to model the population dynamics of a single cohort over a nymphal period having K instars. (In some contexts it may be preferable to break the life cycle into other stages, e.g., oviposition, and pre- and post-oviposition, or egg–larva–pupa–adult.) Thus, we are assuming that insects eggs are hatched and give rise to an initial cohort of nymphs that progress toward adulthood through well-defined stages. The length of time the animal is in each instar depends on the environmental temperature history. There are two inputs to the main part of the model, the micro-habitat temperature T_m (which determine the body temperatures of the predator and prey) and the density S_n of the predator on day n . The predator density S_n involves only the density that affects the prey population in a given stage of development. The model does not include the effect of individuals of a cohort developing at different times.

2.1. Temperature and phenology

In addition to using size (length, weight, or other physical attributes) or age to track an organism's life history, it is common

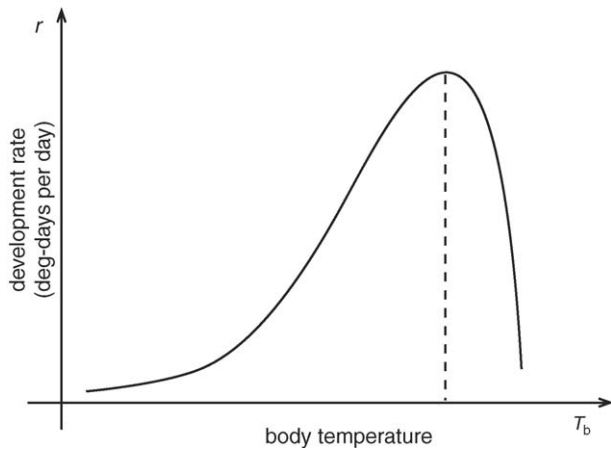


Fig. 1 – A plot showing a typical strongly nonlinear development rate for an insect as a function of body temperature.

to use cumulative development, or phenology, as the structure variable in a physiological structured model. For a thorough description of continuous and discrete physiological models we refer to Auslander et al. (1974), Nisbet and Gurney (1983), Metz and Diekmann (1986), Metz et al. (1988) and de Roos (1997). See also Sharp and DeMichele (1977) for an approach based on temperature-dependent reaction kinetics. Development rates for insects are strongly dependent on body temperature, and these rates at each critical stage in an insect’s life cycle can have pronounced effects on key population parameters. Some models have included temperature as the driving mechanism for these phenological variations; see Wollkind and Logan (1978), Bentz et al. (1991), Wermelinger and Seifert (1999) and Logan and Powell (2001). Through behavioral activities, like adjusting body orientation, some insects achieve temperatures close to that which induces a maximal rate of development (Lactin et al., 1995; Lactin and Johnson, 1996a,b, 1997, 1998). Others (Powell et al., 2000; Jenkins et al., 2001) have inferred that seasonal temperatures can synchronize life cycles. See also Logan and Bentz (1999) and Gilbert et al. (2004).

We measure prey development in degree-days with $r = r(T_b)$ denoting the development rate, measured in degree-days/day; T_b is the body temperature. A typical development rate plot is shown in Fig. 1. At low temperatures the development rate is small; as body temperature increases there is an increased rate up to a maximum value, and then a rapid decrease. This model of degree-day development is nonlinear and valid over the entire temperature range. It is unlike the standard linear model used by biologists which accumulates degree-days by adding up amounts over some temperature threshold. Typically, the linear model is less accurate than the nonlinear model and approximates it only over a narrow temperature range. Operating near the maximal rate entails a risk if the body temperature happens to increase a small amount. At hour k during a day, the insect accumulates $r(T_b(k))/24$ degree-days, where $T_b(k)$ is the body temperature at hour k . Therefore, on day n , depending upon the hourly body temperature, the insect accumulates δ_n degree-days

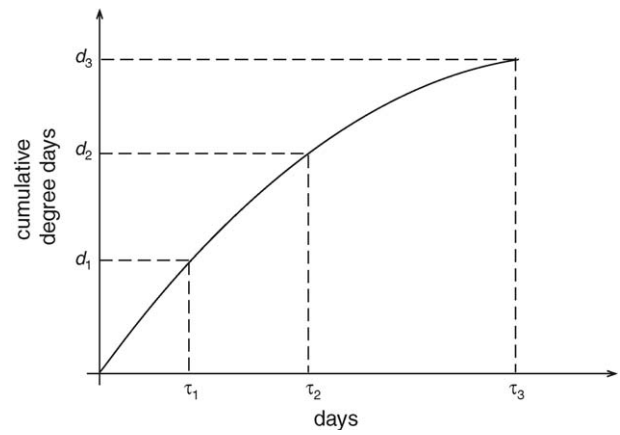


Fig. 2 – A generic plot of the cumulative degree-days vs. time showing the development milestones d_i at times τ_i , $i = 1, 2, 3$. Here there are $K = 3$ instars.

given by

$$\delta_n = \frac{1}{24} \sum_{k=1}^{24} r(T_b(k)). \tag{1}$$

To keep the notation simple we have not indicated that body temperature also changes day-to-day, and hence depends upon n . The cumulative number of degree-days after n days is

$$D_n = \sum_{i=1}^n \delta_i. \tag{2}$$

We denote by d_j , $j = 1, 2, \dots, K$, the cumulative number of degree-days required to complete the j th instar. These quantities have been determined experimentally for many taxa. Hence, the total time to complete development through the j th instar is the first integer τ_j for which

$$D_{\tau_j} \geq d_j, \quad j = 1, 2, \dots, K. \tag{3}$$

Fig. 2 depicts a typical developmental history with these quantities indicated on the plot. The times τ_j are body temperature-dependent; hence, temperature dictates the rate that the dynamics of development occurs. We assume the same development rate function holds over the course of development through each instar, although the model can be adapted to instar-dependent development curves (see, for example, Logan and Powell, 2001). Further, temperature also dictates a nonlinear growth rate of trees in much the same way as presented herein (Schenk, 1996).

The prey dynamics has the form

$$H_{n+1} = H_n - m_n H_n - F(a_n, H_n, S_n), \quad n = 1, 2, \dots, N, \tag{4}$$

where m_n is the daily mortality rate and $F(a_n, H_n, S_n)$ is a predation functional response for the main predator under investigation. The mortality term represents number of prey succumbing each day from random natural causes, such as decreased food quality, disease, environmental conditions, other predators, and so on. The predator functional response contains a temperature-dependent, joint predator–prey activ-

ity period a_n that can increase or decrease the number of predation events each day. This activity period is computed as the time in a day when both predator and prey are active, and it depends upon the hourly temperature. Daily activity occurs on a faster time scale than the model's daily scale, making the model what is referred to as *metered*. The model evolves to day N when development is complete; N , of course, depends upon the temperature history in the environment. Various parts of the model (4) will be discussed below.

The daily mortality rate m_n is assumed to be instar- or size-dependent. Thus,

$$m_n = \mu_j, \quad \tau_{j-1} < n \leq \tau_j, \quad (5)$$

for $j = 1, \dots, K$. That is, μ_j is an assumed constant daily mortality rate for the j th instar. Data for these rates are available for many taxa. The assumption of a constant daily mortality rate within an instar is approximate because some insects have higher mortality rates in the first few days after molting. Lower temperatures will lengthen the instar periods and lead to greater mortality, especially in the earlier instars where daily mortality is high.

2.2. Activity and predation

For predation events to occur, either the predator or the prey must be active; the predator must be hunting and the prey must be susceptible to predation. The activity times of each are temperature-dependent. In this model we assume that there is an overlap, micro-habitat temperature interval $T_{lo} \leq T_m \leq T_{hi}$ where predation can occur. The lower threshold T_{lo} represents, for example, the minimum temperature that prey are active, and the upper threshold T_{hi} represents the maximum temperature that the predator is active. Of course, the thresholds may be interchanged for the prey and the predator. These assumptions can be modified to include temperature zones where the predator is active and the prey is inactive and chance interactions occur (see a study of foraging and risk in Wolesensky and Logan (in press-b)). Fig. 3 shows a generic daily temperature trace indicating the various quantities. The joint activity period a_n for day n is defined as the fraction of the day when the micro-habitat temperature lies in the overlap interval. That is,

$$a_n = \frac{1}{24} \sum_{k=1}^{24} \mathbf{1}_{T_{lo}(k) \leq T_m(k) \leq T_{hi}(k)}, \quad (6)$$

where $\mathbf{1}_B$ denotes the indicator function of a set B , taking the value 0 or 1, depending upon the truth value of the statement B . Thus, the quantity a_n is a metered daily value computed from hourly temperature data. If the daily micro-habitat temperature varies significantly, the activity period can shift dramatically. The factor a_n appears in the predation functional response.

Predation is a key ingredient in the regulation of many insect populations, and predators are often used as a control element to limit pest population sizes. There are many available forms for the functional response, or rate of predation. Depending upon the taxa and hunting tactics of the predator, one form of a response may be preferred over another. In the

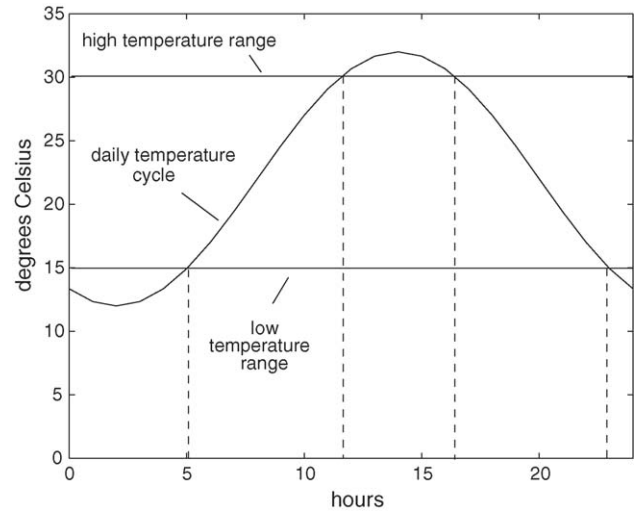


Fig. 3 – Generic plot of the daily temperature and the upper and lower thresholds. The activity period is the time when the temperature lies between the upper and lower thresholds. In the figure the activity period is about 14 h (activity between 5 and 12 and between 16 and 23).

present model we show one method to include temperature effects in predation, namely to modify the classic Holling type II response (Holling, 1959) to include the joint-activity period a_n . See Gilioli et al. (2005) for an alternate method of including temperature through a Gutierrez–Baumgartner response.

To indicate precisely how this modification occurs we briefly repeat the usual argument leading to the Holling type II response (e.g., see Case, 2000, p. 243). We assume a fixed region of area A_r where the prey are randomly distributed, and we assume that a predator enters the area with a given effective search rate A_s and an available time T that must be split into time T_s for searching and time for handling the prey that are subdued. The time scale is on a daily basis. Specifically, we introduce the following quantities with their associated units:

A_r	total area (m^2)
A_s	area searched per time per predator ($m^2/(\text{day predator})$)
T_s	time spent searching (day)
T	total time available for the search (day)
τ	handling time ((day predator)/prey)
h	number of prey (prey)
s	number of predators (predators)
κ	prey captured per prey encountered (prey/prey)
d	detection factor
a_n	daily activity period (day)
m_n	daily mortality rate

The number of prey encountered on a given day, per predator, is the number that come into the area searched, times those detected, or

$$h_e = dT_s A_s \frac{h}{A_r}.$$

The number of prey captured, per predator, is therefore

$$h_c = \kappa dT_s A_s \frac{h}{A_r}$$

Next, the total time T available to a predator is the search time plus time for handling. The latter may include time for digesting the prey or recovering from satiation before embarking upon another search. The time spent handling the prey is proportional to the number of prey captured, with proportionality constant τ , the time spent handling a single prey. Therefore, $T = T_s + \tau h_c$. Substituting into the last equation and solving for h_c gives

$$h_c = \frac{\kappa dT A_s(h/A)}{1 + \kappa d\tau A_s(h/A)}$$

If s is the number of predators in the patch, then the total number captured is

$$\text{total captured} = \frac{\kappa dT A_s(h/A_r)}{1 + \kappa d\tau A_s(h/A_r)} s.$$

In the standard model, the time T is the total time available for the predator to find, subdue, and handle prey. In our modification, this time depends upon the daily temperature cycle and is defined to be the activity period, or $T = a_n$. So a_n is the effective search time on day n . If prey are always available, this time period coincides with the time when the micro-habitat temperature is in the predator's range for hunting. If the prey are also constrained by temperature ranges, then that further reduces the effective time for the hunt. The day-to-day dynamics can be expressed simply as the following balance law: The number of prey on day $(n + 1)$ equals the number of prey on day n , less the number that day dying from random causes and the number dying from predation. Placing subscripts on the various time-dependent quantities, the discrete model is

$$h_{n+1} = h_n - m_n h_n - \frac{\kappa da_n A_s(h_n/A_r)}{1 + \kappa d\tau A_s(h_n/A_r)} s_n,$$

or, in terms of densities,

$$H_{n+1} = H_n - m_n H_n - \frac{\kappa da_n A_s H_n}{1 + \kappa d\tau A_s H_n} S_n. \tag{7}$$

Eq. (7), the basic discrete model, is a first-order, non-autonomous difference equation with a Holling type II functional response, modulated by a daily, temperature-dependent activity period or effective search time.

We remark that if the predator density gets too large, then the right side of (7) can become negative; in that case we set the right side equal to zero, leading to extinction. Secondly, if the model were extended to multiple generations (year-to-year, for example, with over-winter dynamics), then the saturated functional response and the relative constancy of the number of predators can lead to a strong Allee effect; these, coupled with temporal forcing, can have dramatic impacts on long-term population dynamics (Schreiber, 2003). In our model, however, we consider only for a single growing season.

Summarizing, the model equations are (1)–(3) and (5)–(7). We input the hourly micro-habitat temperature over a season and the predator density S_n , which is the density that affects the prey on day n . Then, given the initial density of prey, we can advance the prey density day-to-day using (7). We compute a_n each day from (6) where upper and lower temperature thresholds are specified. The speed that the prey go through their development is given by Eqs. (1)–(3), where the body temperature of the prey is determined from micro-habitat temperatures.

3. Spider–grasshopper dynamics

Because grasshoppers and locusts are insect pests that can have a substantial economic impact on food producers, it is not surprising that numerous studies have been carried out to understand their biology. These studies include feeding patterns and food selection, water and thermoregulation, flight mechanisms and migration, chemical communication systems, and diseases. A compendium of biological mechanisms and behavioral characteristics can be found in the classic treatments by Urarov (1966, 1977). An updated review of newer experiments, theories, and facts about grasshopper biology prior to 1990 can be found in Chapman and Joern (1990), who provide a review of population regulation in grasshoppers, including a general overview of the mechanisms and factors that influence their populations. Certainly, one reason for the lack of quantitative, analytic population models is in the diversity and complexity of their behavior, phenologies, life histories, and interactions with their environment. Suffice it to say that it appears impossible to construct a synthetic view of population regulation in the face of such a diversity of underlying mechanisms. There is simply no blueprint of the factors that determine population numbers, nor even a well-developed theory of population outbreaks.

The situation with spiders is similar. One finds great diversity and complexity in work on arachnids, but little on modeling population dynamics. An excellent resource on spiders is Li and Jackson (1996) where vital data, including developmental rates, for various species of spiders has been compiled and reviewed. We consider only lycosid spider predators, and not birds, robber flies, fungi, parasitoids, and others, in order to analyze a simple, manageable system that can be empirically manipulated to determine reasonable values of parameters and to observe interactions. Lycosid spiders are rangeland, wandering wolf spiders that hunt for prey, and they do not build webs (see Joern et al., in press). Because arthropod predator–prey systems are prevalent, the qualitative results could have some implications regarding temperature dependence in other systems.

Now we apply the ideas of the preceding discussion to spider–grasshopper interactions in rangeland environments. Our model development supports an experimental program in Western Nebraska and in the laboratory to understand climate effects on pest dynamics in these ecosystems. It is well known that populations of grasshoppers can grow to the point of outbreaks, but not in all years (Joern and Gaines, 1990). Grasshoppers have a wide range of natural enemies, including birds, other insects, fungi, parasitoids, and spiders. Some of these affect only certain stages; for example, one estimate is that birds

regularly remove 25% of the adult grasshoppers in the late summer in certain sand hills grassland sites. Various experiments and observations over the years have led to estimates of the predation effects, but there have been no attempts to develop a mathematical model that leads to quantitative predictions of population levels, much less temperature-influenced effects (Joern and Gaines, 1990). We focus on a single predator, the wandering wolf spider (lycosidae). Although spiders, which are multiphagous, are not a major controlling predator in outbreak years, they can play an important role in limiting prey populations when at lower densities (Belovsky and Joern, 1995). The predation interaction is also stage-based in that spiders of certain sizes prey only upon grasshoppers in certain instars.

We develop a one-season, cohort model, with temperature-dependent dynamics. We remove much of the complexity by focusing upon simple systems that may be controlled in laboratory or field environments. The goal is to make qualitative predictions about the effects of spider predation, and not to compute exact population numbers. More precisely, we concentrate on computing sensitivities to changes in environmental weather quantities like mean daily temperature, daily temperature amplitudes, and solar power index.

3.1. Temperature and phenology

The model inputs the micro-habitat temperature T_m to calculate activities and the prey body temperature T_b to calculate phenology and development of the grasshopper. Body temperatures of grasshoppers have been measured as functions of their micro-habitat temperature T_m , and in this model we

use the Harrison and Fewell (1995) formula ($R = 0.88$)

$$T_b = \begin{cases} T_m, & T_m < 17, \\ -0.34T_m^2 + 2.48T_m - 7.01, & T_m \geq 17. \end{cases}$$

A plot of T_b versus T_m is shown in Fig. 4c. Below 17°C the body temperature is close to that of the micro-habitat; for higher temperatures the grasshopper thermo-regulates by orienting its body to raise their body temperatures. Field site data (Danner and Joern, 2004) were fit to determine a nonlinear regression equation for the micro-habitat temperature T_m as a function of the air, or ambient, temperature T_a and the solar power density W (W/m^2) falling on the habitat. The density W changes hourly and is modeled by a function that is zero between 6 p.m. and 6 a.m., and a positive, concave-down, parabola between 6 a.m. and 6 p.m., with maximum W_{max} . The ambient temperature was taken at 2 m above the ground, and the micro-habitat temperature at ground level. Vegetation in the region varies from 0-45 cm high. (It is clear that the type of canopy strongly affects the relation between micro-habitat and ambient temperatures.) The regression formula is $T_m = 6.214 + 0.327T_a + 0.011W + 0.017T_a^2$, with $R^2 = 0.92$. The hourly ambient air temperature $T_a(k)$ on a fixed day n is modeled by a periodic, cosine function

$$T_a(k) = \bar{T}_a(n) + A \cos \frac{(k - 14)\pi}{12}, \quad 0 < k < 24,$$

where $\bar{T}_a(n)$ is the mean, ambient air temperature on day n . Common, sinusoidal models for temperature represent only an approximation for the daily temperature fluctuation. Alternately, the daily temperature could be made more precise

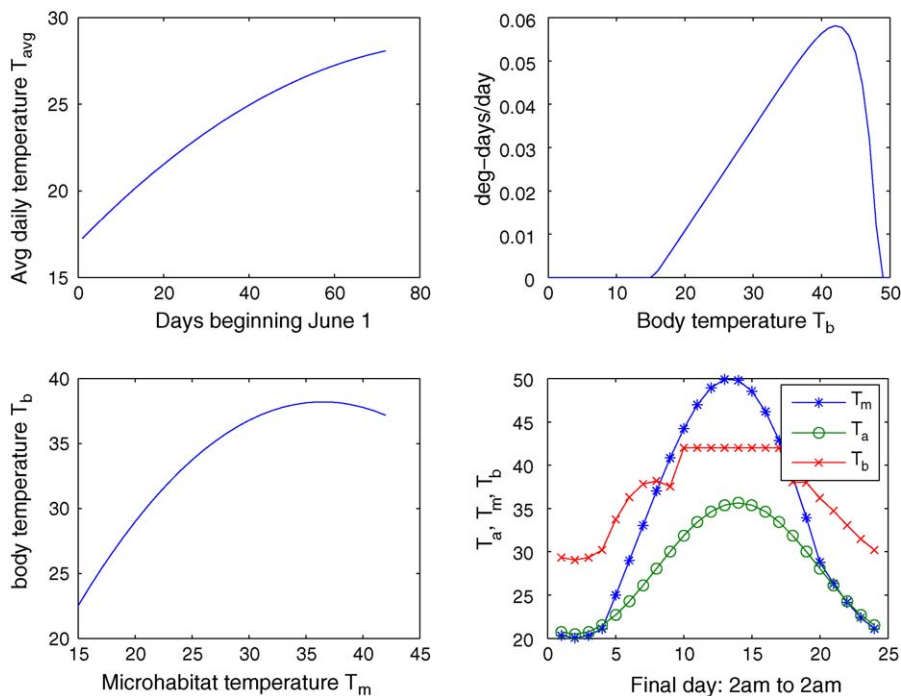


Fig. 4 – Baseline simulation showing the average daily temperature over the season, the nonlinear development rate vs. body temperature, the body temperature of the grasshopper as a function of micro-habitat temperature, and a comparison of body, air, and micro-habitat temperatures on the final day of development.

by including an exponential lag phase after sunset, with the sinusoidal variation during daylight hours. Even differently, we could use exact field site temperature data, which is available. However, for the purposes of this study, we avoid the complexity of more detailed models, even stochastic models, and use the simple sinusoidal model. This assumption will not distract from the basic problem of studying predation responses. Our simulations do not produce exact population responses, but rather examines changes from a baseline calculation. Further, daily temperature amplitudes A can also vary as daily temperatures increase through the season. But weather data over a 3-month period in the rangeland environment in our study shows little variation in average daily amplitude. The model can be easily modified to include more detailed temperature and amplitude expressions, even including random processes.

The mean daily air temperature $\bar{T}_a(n)$ can also be obtained from field site data for a single year, but rather we take an average value from the region compiled by the U.S. Weather Service (2004). The average daily temperature on day n , computed over a 30-year period for the dates 1 June–30 September 30, can be fit by the quadratic $\bar{T}_a(n) = 17.01 + 0.2547n - 0.0014n^2$, with $R^2 = 0.96$. See Fig. 4a. The average daily amplitude over a short, 3-month period A is $A = 7.58^\circ\text{C}$. Through these formulae, the average daily temperatures lead to body temperatures of the insect. Plots relating the hourly air, micro-habitat, and body temperatures are shown in Fig. 4d (on the final day of development). There does not seem to exist similar data for lycosid spiders, and so we assume the spider has the temperature of the micro-habitat T_m .

A typical rangeland grasshopper has $K = 5$ nymphal stages. Its development rate r , of which a generic form is shown in Fig. 1, is a function of body temperature. We use Lactin et al. (1995) modification of the Hilbert and Logan (1981) equation

$$r(T_b) = e^{\alpha T_b} + e^{[\alpha\beta - (\beta - T_b)/\Delta]} - \lambda,$$

where the fitted parameters are given by $\alpha = 0.002245$, $\beta = 54.872728$, $\Delta = 2.426034$, $\lambda = -1.035138$. This formula fits the nymphal stages of *M. sanguinipes*, and a plot of this specific development rate is shown in Fig. 4b. We take $r = 0$ when the right side evaluates negative. The maximum development rate of 0.059 day-degrees per day occurs at 42°C . At 36°C the rate is 0.0486, and it requires approximately 12 days, or 0.58 degree-days, to complete an instar. Therefore, the cumulative degree-days required to pass through the nymphal stages is $d_5 = 2.9$. In general, $d_k = 0.58k$, $k = 0, \dots, 5$. The j th instar is defined by the range

$$0.58(j - 1) < D_j \leq 0.58j, \quad j = 1-5.$$

Laboratory data compiled by Hilbert and Logan (1981) shows a variation in the nymphal period from about 20 days (at 40°C) to 80 days (at 21°C). Our simulations, based on field temperatures, are nearer the lower temperature range.

3.2. Mortality and food quality

It is difficult to obtain data on grasshopper natural mortality, even under ideal conditions. Different studies, some of which

are performed in the laboratory and others in the field, often give different values (Joern and Gaines, 1990; Oedekoven and Joern, 1998; Danner and Joern, 2004) because of variations in the environment, in location, and in the species. For our simulations we take the following daily mortality rates for the five instars:

$$\begin{aligned} \mu_1 &= 0.067, & \mu_2 &= 0.050, & \mu_3 &= 0.039, \\ \mu_4 &= 0.022, & \mu_5 &= 0.005. \end{aligned}$$

The daily rates are based upon measured 10-day instar mortality rates of 50, 40, 33, 20, and 5%, respectively. In reality, mortality for grasshoppers varies within each instar with higher risk immediately after molting, so constant values within an instar represent an approximation. The sources of natural mortality include various pathogens (protozoa, viruses, fungi, bacteria, and others) as well as lack of fitness through demographic variation (Urarow, 1966, 1977; Streett and McGuire, 1990).

In the application of the model to grasshoppers, we can include an additional factor in the natural mortality term, namely the quality and quantity of plant foods. Both can have a marked influence on grasshopper population and life history parameters. It is often the case that food is abundant; but food quality may change significantly over a growing season and dramatically affect survivorship. Food quality is related to percent nitrogen, which in turn is related to percent protein in the diet. A rule of thumb is that the nitrogen availability in the leaf decreases from about 3–5 to 1% over a summer, which we take to be 100 days. The decrease is nearly linear, with a slight upward curvature, until it reaches the bottom point (August), at which time there is no further change. However, it can increase slightly with late summer rains and slightly cooler temperatures in September. This has been measured directly, but not published formally. Therefore, to model this decreasing food quality effect, we introduce a daily food quality index by the formula

$$q_n = e^{-n \ln 3/100},$$

which decreases geometrically, having the value 1 at $n = 0$ and value $1/3$ on day $n = 100$. We include this factor in the natural mortality rate in a simple way by an inverse proportion. Specifically, the term $m_n H_n$ in (7) is replaced by $q_n^{-1} m_n H_n$. Therefore, as food quality decreases over the season, there is an increase in natural mortality. Over very short developmental periods the food quality factor is nearly constant. Field fertilization could also affect this factor. In simulations, which are discussed later, we take $q_n = 1$ and assume no variation in food quality.

There are other feeding-related factors not included in this model. For example, when food quality is low, insects often compensate by increasing their consumption rate, if environmental conditions permit. Furthermore, feeding is also affected by the presence of predators. Prey vigilance may reduce predation but increase mortality through reduced feeding. Although this has been proposed for large herbivores, like elk under pressure from wolf predators (Brown et al., 1999), there is evidence (Beckerman et al., 1997; Danner and Joern, 2003a,b) that some grasshoppers may seek refuge and reduce food consumption in the presence of spiders, thereby being unable to

meet nutritional demands (Logan et al., in press; Wolessky and Logan, in press-b). Finally, we do not include spatial effects where, for example, prey can move to a different patch when predators are present. Discussion of these modifications is a subject for future research.

3.3. Predation and activity

The parameters in the modified Holling type II response depend upon the hunting tactics of the spider and have not been generally determined. Recent laboratory and field experiments (Joern et al., in press), however, have led to estimates for some of these parameters values.

Spider densities and sizes over a growing season were estimated from field experiments at Cedar Point Biological Station in western Nebraska using pitfall traps and a mark-recapture technique. At two sites the densities of wolf spiders were estimated to be 0.28 and 0.19/m². The average size of the spiders captured over the summer remained nearly constant (about 11 mm with a range 5–23 mm). Two periods of spider activity were distinguished, early morning and late evening; overall, the probability of observing spider activity was about three times greater if the micro-habitat temperature was less than or equal to the ambient air temperature (Joern et al., in press). Handling times were estimated by averaging observed handling times in a laboratory arena over which a suspended video camera (EthoVision) recorded predation events. Trials were conducted on two groups of spiders, satiated and starved. For starved spiders there was less time to a predation event (0.5 h versus 1.3 h) and the handling time was longer (about 4.6 h versus 2.6 h).

Based on these observations, we take the handling time to be 3.6 h ($\tau = 0.15$ days), and $\kappa d = 0.5$. Grasshoppers were observed to be present in the micro-habitat at all times, so we base the activity levels on spider activity alone. The estimated activity temperature range of spiders is $T_{lo} = 10^\circ\text{C}$, $T_{hi} = 20^\circ\text{C}$, corresponding to morning and evening times. Finally, the search rate is estimated (on the lower end) to be $A_s = 100 \text{ m}^2/(\text{day predator})$, which is the least certain quantity in the model, and it has not been measured for wandering, rangeland, wolf spiders that do not build webs. For large prey densities the predation rate approaches its maximum value a_n/τ . In spider–grasshopper interactions, for example, if the total available period that day is 9 h ($a_n = 9/24$), when the micro-habitat temperature is in the activity range, then the maximum predation rate, per spider, is 2.5 prey per day. This number is representative of the average number often quoted by experimentalists. As noted above, handling times may be greater when grasshoppers are at lower densities, and smaller at higher densities, so in a more refined model the handling time could be expressed as a function of grasshopper density.

The spider density preying upon grasshoppers in a given instar is difficult to determine. It is estimated that the maximum size of the grasshopper taken is a linearly increasing function of the spider size. In the simulations, we assume first-instar nymphs are too small for predation, and so $S_1 = 0$. Therefore, natural mortality is the only risk factor in the first instar. As size increases, we assume the predation factor becomes appreciable. We take spider densities (spiders per m²) to be $S_2 = 0.005$, $S_3 = S_4 = 0.01$, $S_5 = 0.005$. The drop-off in the

last instar is assumed to result from the small availability of large wolf spiders to prey upon the large grasshoppers. In fact, bird predation may be a factor in this instar, but we do not consider that effect. Furthermore, we are only considering a single cohort and are ignoring effects caused by spider predation on other cohorts that are present. Therefore our model is an ideal case, which can be studied in a laboratory setting, where only one cohort is present. Understanding the predation dynamics of a cohort is the first step in developing a general theory. Generally speaking, individuals terminate development at different times, and there is a distribution of degree-days required to become mature. Individuals on the tail end of that distribution may have a higher rate of predation, but we do not complicate the model with this effect. Finally, the uncertainty of these spider densities do not dramatically affect our goal of computing changes in mortality under environmental variations. Effectively, we are assuming spider density is fixed and we are assessing changes in prey populations due to temperature changes. The spider density is a linear factor in the predation rate and its variation will affect the results accordingly.

3.4. Simulations and results

Arthropod predator–prey interactions are complex, and the best hope for a mathematical model is that it can provide a conceptual framework for a discussion of the interactions and possibly suggest experimental strategies to extract detailed biological information. Through simulations we can make qualitative statements about sensitivity to changes in the parameters, or how much and in what direction output quantities are changed when input parameters are varied. Through a specific choice of input parameters we create a benchmark, or baseline calculation, against which we can compare the other simulations.

The base values we select for the hunting parameters are given as follows: $A_s = 100$, $\kappa d = 0.5$, $\tau = 0.15$, $T_{lo} = 10$, $T_{hi} = 20$. The low-high temperature range is for the spider predator; we assume the prey is always susceptible to predation. The baseline environmental parameters are the maximum daily solar power index (a measure of sunlight), the average daily temperature amplitude, and the average daily temperature on 1 June: $W_{max} = 1000$, $A = 7.58$, $T_a = 17$. The average daily temperature increases over the season, but the amplitude and solar index do not vary from day to day. The initial density of the cohort is 20 grasshoppers/m². The remaining model parameters are given in the preceding sections, and we assume $q_n = 1$ (no food quality factor). The calculated nymphal period and end-of-season-survivorship for the benchmark calculation are

- nymphal period = 72 days,
- survivorship (no predation) = 4.5%,
- survivorship (with predation) = 3.3%,

where the survivorship is the fraction of the initial density (20 m⁻²) that survives the nymphal period. In the baseline calculation, spider predation accounts for an additional 1.2% of mortality. The subplots in Fig. 5 show the results of the benchmark calculation: the cumulative degree-days over the nymphal period and the survivorship curve.

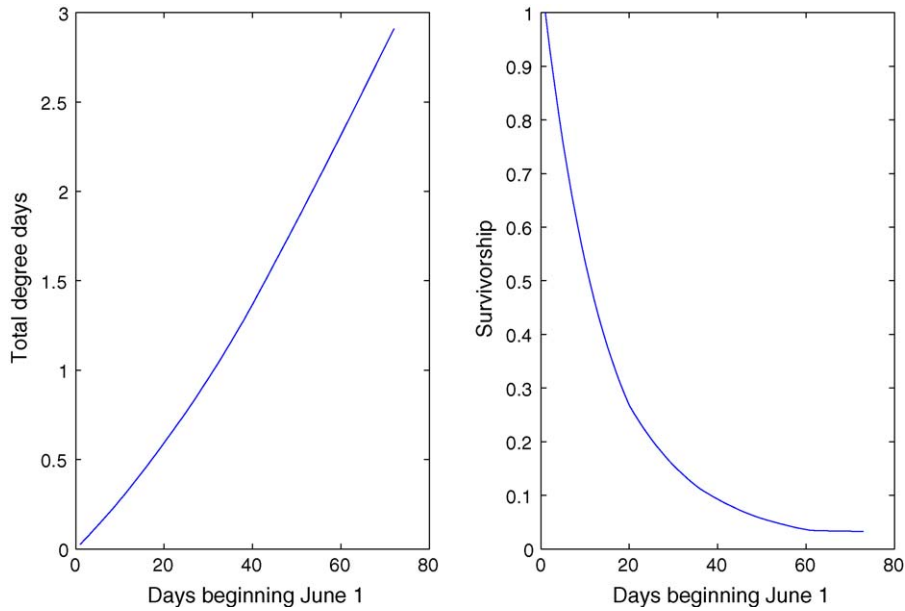


Fig. 5 – Cumulative degree-days and survivorship for the baseline values.

The hunting parameters do not affect phenology or the length of the nymphal period, and they have only a small effect on changes in survivorship. This is because the half-saturation in the Holling response is 0.13 grasshoppers/m², well below the computed density. Thus, at the densities examined, the predation rate is near its maximum value a_n/τ , and this means that only the temperature-dependent activity period will strongly affect the daily predation rate.

Fig. 6 shows the effect of varying the average daily temperature on 1 June, with the remaining parameters retaining their baseline values. Increasing the temperature on 1 June could also correspond to an earlier hatching date for the grasshopper population. Over the given range, the plots show that if the average daily temperature increases by 6 °C, then the

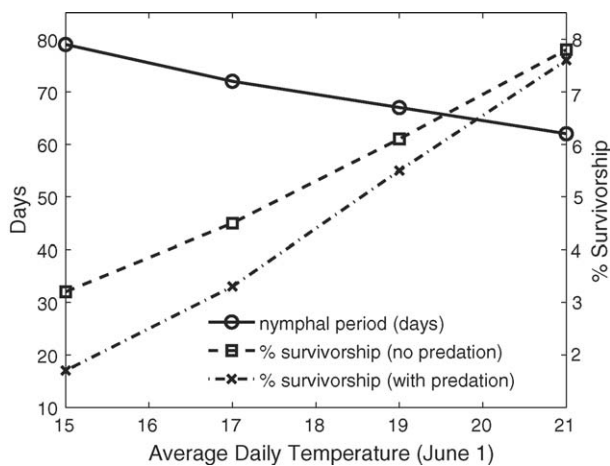


Fig. 6 – Plots of the nymphal period and survivorship with, and without, predation, over a range of mean daily temperatures. As mean temperatures increase, predation is a decreasing effect.

nymphal period decreases 17 days, or nearly 3 days/°C. Predation becomes much less of a factor at higher temperatures because of the decrease in the activity period of the spider predator. The effect of an average daily temperature shift of a few degrees can be dramatic, with natural mortality being the major contributing effect. At 15 °C predation decreases survivorship by 47%, while at 21 °C it decreases it only 2.5%. Therefore, at higher average temperatures fewer numbers of grasshoppers are being consumed. From the predator's view, this means generalist predators like spiders must seek alternate food sources.

Fig. 7 shows the effect of varying the daily temperature amplitude, again with the remaining parameters retaining their baseline values. Over the calculated range, increasing the amplitude of daily temperature oscillations predicts an increase in the development period with an accompanying decrease in survivorship. Comparing the results with those in Fig. 6, we observe that increased amplitude increases the nymphal period, while increased temperature decreases the nymphal period. More importantly, whereas increased mean temperatures decrease the predation, increased amplitudes, which measure variation, magnify the effects of predation (from 13 to 37.5%), and larger numbers of grasshoppers are being consumed. Thus, extrapolating, we may conclude that more erratic daily temperature variations through the season results in less favorable conditions for grasshoppers.

Fig. 8 shows the effect of varying the average daily solar power index, W_{max} . This factor is related to the amount of sunlight falling on the habitat each day, and it affects the microhabitat temperature. Increasing W_{max} decreases the development period and leads to a modest increase in survivorship; it does not appreciably affect predation levels.

It is interesting to simulate the extreme cases when either positive or negative factors combine. By increasing the average daily temperature and power density, while decreasing the variation of the daily cycle (taking $W_{max} = 1200$, $\bar{T}_a(0) =$

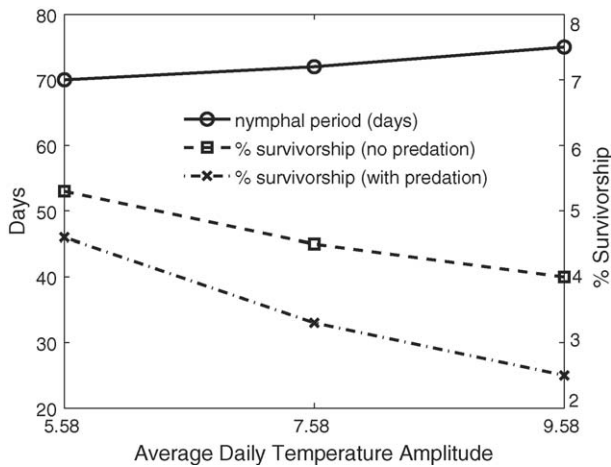


Fig. 7 – Plots of the nymphal period and survivorship with, and without, predation, over a range of average daily temperature amplitudes. As amplitudes increase, the effect of predation increases only slightly.

21, $A = 5.58$) we obtain

- nymphal period = 60 days,
- survivorship (no predation) = 8.7%,
- survivorship (with predation) = 8.7%.

Thus, there is a significant decrease (29%) in the nymphal period with a negligible contribution to predation. At the other extreme, taking $W_{\max} = 800$, $\bar{T}_a(0) = 15$, $A = 9.58$, we obtain

- nymphal period = 85 days,
- survivorship (no predation) = 2.5%,
- survivorship (with predation) = 0.9%.

Therefore, predation in this case is more of a factor than in the opposite extreme. When positive or negative feedbacks combine, as is possible when there is strong environmental stochasticity, significant changes can occur. We summarize our findings in the next section.

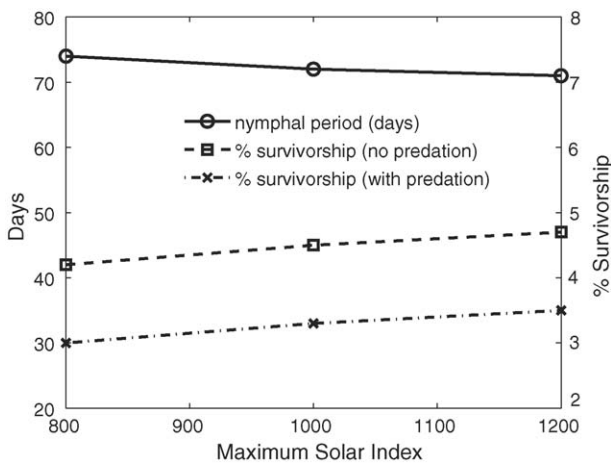


Fig. 8 – Plots of the nymphal period and survivorship with, and without, predation, for a range of maximum solar index.

4. Summary and conclusions

In the many studies on arthropod predator–prey systems there have been few that address and quantify temperature effects on the interactions. Moreover, in spite of the large number of experimental and statistical studies of grasshopper populations, there have been few detailed quantitative models of the dynamics. In this paper we have developed a discrete, metered, cohort model of grasshopper survivorship and development based upon natural mortality, which depends on both the development stage and upon spider predation. Temperature indirectly affects the natural mortality rate through lengthened or shortened developmental milestones (instars); in the model, mortality rates are time, stage, and temperature-dependent. Temperature effects on predation in this specific system are included directly through an activity factor in a temperature-mediated Holling type II response. The activity factor, which is the fraction of each day available to the predator for hunting and handling prey, depends on the daily temperature variation. Including temperature in this unique manner may be applicable to other predator–prey interactions. In those systems temperature variations may shift the activity periods of both predator and prey to cause significant changes in predation rates. The model can address these general issues if system-appropriate predator densities are imposed during the prey developmental periods. However, in the spider–grasshopper ecosystem we examined, field experiments show that spider densities and size distributions are nearly constant through the nymphal period of the grasshoppers. There has been no attempt to resolve the dynamics of the predator population.

In summary, environmental temperature variations predict changes in population densities and phenology. The key parameters in the model are the average daily temperature, the amplitude of the daily temperature around its average (the high and low), and the maximum solar power density W_{\max} reaching the surface each day. Increasing the average daily temperature significantly increases the final density of insects at the end of the nymphal period while shortening the nymphal period; but it decreases the effect of predation, both relatively and numerically. The result of an average daily temperature increase would be a large number of adults at an earlier time, thereby lengthening the period of reproduction of mature adults in late summer. This can lead to significant increase in grasshopper populations for the next year if over-winter conditions are ideal for egg survival. Increasing the variation, or amplitude, of the daily temperatures has a mild effect on lowering densities and lengthening the nymphal period, but the effect on predation is increased significantly.

For the ecosystem examined in this work, the simulations show that some arthropod predators may play only a small role in the population dynamics of grasshoppers compared to the mortality suffered by slowed development and natural mortality. We have not examined the effects of predators, like birds, which may have dramatic effects upon adult populations in late summer and fall. The parameters defining the hunting characteristics of the predatory spider are robust compared to the parameters that characterize environmental conditions. Thus, this simple model seems to confirm

that climate conditions are the major influencing factors in affecting nymphal populations of grasshoppers, and predation effects become important only when temperatures are lower and have strong variation. Although not included in this model, one can conjecture that catastrophic climate events (floods, excessive rainfall, freezes and cold spells) and bonanza events (high temperatures with little variability, seasons with very high food quality) play a significant role, as do fungal and parasitoid effects, which may be driven by temperature and moisture conditions. Overall, grasshopper outbreaks may also be attributable to over-winter survivorship, which again may have a strong weather component.

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