

ACCOUNTING FOR TEMPERATURE IN PREDATOR FUNCTIONAL RESPONSES

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ABSTRACT. A rational mechanism that integrates temperature-mediated activity cycles into standard predator functional responses is presented. Daily temperature variations strongly influence times that predators can search for prey, and they affect the activity periods of prey, thereby modifying their detection by predators. Thus, key parameters in the functional response, the search time and the detection, become temperature-dependent. These temperature mediated responses are included in discrete-time population growth models, and it is shown how environmental temperature variations, such as those that may occur under global climate change, can affect population levels. As an illustration, a logistic growth model with a stochastic, temperature-dependent predation term is examined, and the response to both average temperature levels and temperature variability is quantified. We infer, through simulations, that predation and prey abundance are strongly affected by mean temperature, temperature amplitudes, and increasing uncertainty in predicting temperature levels and variation, thus confirming many qualitative conclusions in the ecological literature. In particular, we show that increased temperature variability increases oscillations in the system and leads to increased probability of extinction of the prey.

1. Introduction. Global climate change is a central issue in ecology, and it is important to assess how anticipated temperature changes might affect trophic interactions, food webs and natural resources (Dunham [1993], Kareiva [1993], Harrington et al. [1999], Walther et al. [2002], Newman [2003], Joern et al. [2005]). On a local spatial

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scale, temperatures may increase, decrease, or become less predictable. Many experimental studies, documented in an extensive literature, have already confirmed the scope and variety of these effects on ecosystems, communities, and populations (Burns [2000] contains a bibliography up through year 2000). For example, temperature significantly affects poikilothermic animals, especially their phenology (Bentz et al. [1991], Li and Jackson [1996], Gilbert and Ragworth [1996], Logan and Bentz [1999], Wermelinger and Seifert [1999], Powell et al. [2000], Logan and Powell [2001], Jenkins et al. [2001], Gilbert et al. [2004], Logan et al. [2007]). The phenological fluctuations can alter the emergence time of an insect and shorten its nymphal period, thereby leading to lengthened periods to reproduce as adults, or they may lead to shifts in trophic interactions that reduce, or amplify, predation opportunities and events (Wollkind and Logan [1978], Rochat and Gutierrez [2001]).

There are standard methodologies to include random environmental effects, including bonanza and catastrophic events, in predator-prey models. These general random effects can include rainfall, moisture, floods, droughts, food quality, freezes, and temperature variations as well. One idea is to develop a stochastic model *a priori*, by defining a process based on a probability model, e.g., a Markov process or a binomial process. Another approach is to modify parameters, e.g., the growth rate, in a given deterministic model by making it a random variable chosen from some distribution. (Many examples are documented in, for example, Renshaw [1991], Roughgarden [1998], Caswell [2001] and Allen [2003]). Further, environmental or demographic stochasticity can be included into a known deterministic model by adding noise on logarithm or square root scale, e.g., Cushing et al. [2003]. All of these methods lead to stochastic difference or differential equations, where environmental stochasticity is treated as a general quantity but not necessarily determined from a single, specific mechanism. The idea in this communication is to add stochastic temperature variations in a specific, mechanistic manner by modifying the search time in the predator's functional response. Our model generalizes other models where risk and foraging are chosen as binomial random variables in discrete growth and fitness models, e.g., see Luttebeg et al. [2003], Wolesensky and Logan [2007], and it is applicable to general classes of trophic interactions.

More specifically, predator-prey relationships are one of the key factors that influence population regulation. Mathematical models of these interactions focus on the predator's functional response, which contains quantities that define the predator's hunting characteristics, such as search time, search rate, encounter rate, detection ability, and capture rates. In the literature, simple mechanistic models of predation mechanics that include specific temperature effects are limited. In these works the temperature is a parameter taking on different constant values, but does not vary in time as in the model we are proposing. Mack and Smilowitz [1982] include temperature dependent handling times and search rates, Xia et al. [1999a] examine temperature dependent mortality in aphids, Bianchi et al. [2004] have studied the emergence of lady beetles and their interactions with aphids, and Drechsler and Settele [2001] study leafhoppers and hunting spiders in rice ecosystems at different constant temperatures. In the same vein, Xia et al. [1999b, 2003] measure functional responses at different constant temperatures in an aphid-ladybeetle system. Gilioli et al. [2005] look at a temperature dependent response in greenhouse environments with fruit flies and a predaceous fly; we comment further on this paper in subsection 2.2. Finally, Rinke and Vijverberg [2005] study temperature effects in *Daphnia* populations.

In this paper we present a rational mechanism that introduces a time dependent temperature dependence into a predator's functional response and therefore into the mechanics of predation. The basic observation is that over a short time scale temperature affects the activity time of the predator or the prey, or both. Higher temperatures may be favored by the prey, for example, while warmer environments may reduce the activity of the predator. Changes in temperature levels may cause activity times to shift so that predation events increase or decrease. For example, one trophic interaction for which this effect is documented occurs in grasshopper-lycosid spider interactions in rangeland environments (Joern et al. [2006]). In this paper we show how temperature-dependent activity times lead to modifications in the search time and detection rate of the predator, and therefore the encounter rate. We take a general approach and study a generic predator-prey interaction, rather than focusing upon specific species. As an illustration, we examine a discrete logistic growth model with a temperature-dependent predation term, and we simulate the response

of the system for changes in temperature level (average temperature) and variability (measured by daily amplitudes). The temperature input is stochastic and defined by a first-order, autoregressive process.

Time for the discrete model is measured in days. However, temperature-dependent activity factors depend upon behavior of the predator and prey on a shorter time scale, namely, hours during a day. This makes the model *metered*, where daily effects are computed on a finer time scale, and the resulting time-dependence in the predation response leads to a nonautonomous difference equation for prey abundance. This time scale is appropriate for many arthropod systems, for example, where development is on the order of days or weeks, and life histories are over a season. It also may apply in interactions between poikilothermic predators and other prey, where the predator's hunting activity is driven by temperature, e.g., reptiles and small mammals, or poikilothermic prey and endothermic predators, e.g., insects and birds. We do not address the possible extension to other trophic interactions, say between mammals, where both species are endothermic and less affected by temperature variations. The time horizon is a season of a few years. Further, we develop only a discrete-time model; the extension to continuous-time models (differential equations) is a straightforward modification of the discrete case.

By definition, a predator's functional response is its consumption rate, measured in prey per time, per predator. We focus on Type I and Type II responses. By a Type I response, we refer to the classic Lotka-Volterra model where the predation rate is a linear function of prey density. The Type II response is the classic disk equation of Holling [1959] that saturates at a constant value in the limit of increasing prey density. Interpreted in terms of kinetics, the Type I and Type II responses represent first order, mass-action kinetics, and Michaelis-Menten kinetics, respectively. Under temperature dependence, the modified responses are time-dependent and the dynamics is not autonomous; Type II responses do not saturate at a constant value. Hassel [1978] and Murdoch et al. [2003] are two of the many comprehensive resources that may be consulted for traditional approaches to consumer-resource dynamics. We follow a detailed derivation, similar to that presented in Case [2000, Chapter 11], in developing our model, to indicate precisely where temperature and joint activity levels enter into the mechanics of predation, and therefore to a temperature-mediated predator functional response.

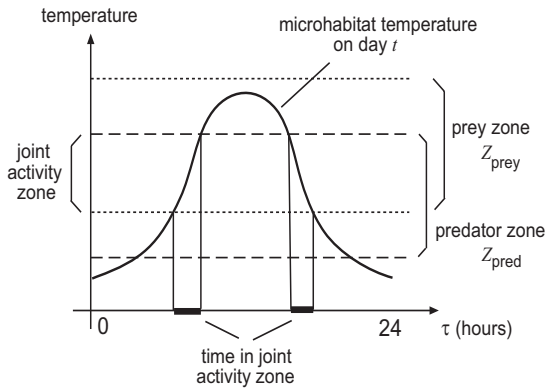


FIGURE 1. Depiction of the hourly microhabitat temperature $\theta_m(t, \tau)$ on day t . The prey and predator activity zones Z_{prey} and Z_{pred} are shown, along with their intersection, which is the joint activity zone: $\theta_l \leq \theta_m(t, \tau) \leq \theta_u$. The microhabitat temperature shown in this figure is sinusoidal, but any daily input temperature is possible. Observe that, as the microhabitat temperature curve shifts upward or downward, the time in the joint activity zone changes.

The key questions we pose, in the context of global climate change, deal with the effects of increased and decreased mean temperature, or increased variability, meaning less predictability or certainty. How do these temperature changes affect predation and population abundance? For example, do outbreaks or extinctions occur when fluctuations are greater? We give possible answers to these questions by performing simulations on a model reptile-small mammal interaction. The goal, consistent with the philosophy expressed by Smith [1974, p. 35], is not to predict actual population abundance, but rather to investigate the change from a baseline simulation when temperature parameters are varied. The assumption is that a comparable change will occur in the behavior of the actual ecological system.

2. Discrete time model.

2.1. *Type I response.* We consider a discrete time model where the time t takes values $t = 0, 1, 2, 3, \dots$, measured in days, and the area of activity A is fixed. The subsequent discussion refers to several quantities whose description and dimensions are given in Table 1. The setting is a general predator-prey system. On day t we suppose the

TABLE 1.

quantity	name	dimensions
n_e	prey encountered by a single predator	prey \cdot predator $^{-1}$
n_c	prey captured by a single predator	prey \cdot predator $^{-1}$
N_t	number of prey at time t	prey
P_t	number of predators at time t	predator
A	fixed area	area
A_s	search rate	area \cdot predator $^{-1} \cdot$ day $^{-1}$
T	total time available	day
T_s	total time searching	day
T_h	total time handling	day
h	time to handle a single prey	day \cdot prey $^{-1} \cdot$ predator
d	fraction detected of those encountered	dimensionless
k	fraction captured of those detected	dimensionless
r	prey growth rate	dimensionless
K	prey carrying capacity	prey
s_t	temperature dependent search time	day
$\theta_m(t, \tau)$	temperature at hour τ on day t	degrees C
θ^*	average yearly temperature	degrees C
a	average yearly temperature amplitude	degrees C
α	autocorrelation of avg. temperature	dimensionless
β	autocorrelation of temp. amplitude	dimensionless
σ_1	standard deviation of avg. daily temp.	degrees C
σ_2	standard deviation of daily amplitude	degrees C
$[\theta_l, \theta_u]$	temp. interval where predation occurs	degrees C

area A contains N_t randomly placed prey. A single predator enters the region and searches for prey at the rate A_s . For example, we may take $A_s = rv$, where r is a characteristic length of the sensory field of the predator and v is the speed of the search. The expected number of prey encountered in time T_s is

$$n_e = A_s T_s \frac{N_t}{A},$$

where T_s is the time spent searching on day t . Not all prey encountered will be detected or captured. If d is the fraction detected and k is the fraction of those detected that are captured, then the expected number captured on day t is

$$(1) \quad n_c = kdA_sT_s \frac{N_t}{A}.$$

We are assuming that those captured are actually those subdued and killed. Additional factors may be included to distinguish these differences.

We now show how temperature fits into the dynamics. The idea is to include temperature in the model by modifying the encounter rate. The key observation is that encounters are affected by activity times of the predator and prey. Many animals, especially poikilothermic animals, have upper and lower temperature thresholds that define times of activity. For example, research with wolf spiders (lycosids) in grassland environments indicate that spiders are active in the early morning and in the evening, but they avoid hotter temperatures during midday (Joern et al. [2006]). In essence, both predator and prey must have overlapping times of activity so that predation events can occur; or, their activity times must intersect. Daily temperature variations can shift activity zones and therefore alter the rate of predation events that occur.

The overall functional response, based on encounter rate, is a characteristic of the predator. We include the predator's activity time in its search time, which is a predator attribute. We assume there are upper and lower temperature thresholds of activity, and above and below temperature thresholds the predator will have diminished searching capacity. The detection factor d represents the predator's efficiency in detecting the prey present in the searched area. However, it is clear that d may depend upon the physical environment and, as well, the behavioral characteristics of the prey. For example, in grasshopper populations, d depends upon the physical structure of the searched area A , whether it is dense forage or open grassland. It can equally depend upon the prey's behavioral characteristics. For example, prey vigilance affects the ability of predators to find prey, e.g., see Houston et al. [1993] or Brown et al. [1999]. In the same way, we regard the prey's activity time as affecting detection; if prey are inactive, or quiescent, an active predator may not detect their presence.

More precisely, let the hourly microhabitat temperature on day t be prescribed by $\theta_m(t, \tau)$, $0 \leq \tau \leq 24$, as shown in Figure 1. The temperature activity zones for predator and prey are indicated. The temperature zone Z_{prey} of prey activity lies between lower and upper threshold temperatures θ_l^{prey} and θ_u^{prey} , while the zone Z_{pred} of predator activity lies between θ_l^{pred} and θ_u^{pred} . The actual search time for the predator on day t is the time that the microhabitat temperature $\theta_m(t, \tau)$ lies in zone Z_{pred} , between θ_l^{pred} and θ_u^{pred} . In symbols,

$$\text{Search time} = \frac{1}{24} \text{meas} \left\{ \tau : \theta_l^{\text{pred}} \leq \theta_m(t, \tau) \leq \theta_u^{\text{pred}}, 0 \leq \tau \leq 24 \right\}.$$

Here, “meas” is the measure, or length, of the time the microhabitat temperature is in Z_{pred} . Now we assume prey are detected only if they are active; that is, predation can occur only when the microhabitat temperature is in the prey zone $Z_{\text{prey}} : \theta_l^{\text{prey}} \leq \theta_m(t, \tau) \leq \theta_u^{\text{prey}}$. The joint activity zone Z , the intersection of Z_{pred} and Z_{prey} , is an interval

$$(2) \quad Z : \theta_l \leq \theta_m(t, \tau) \leq \theta_u,$$

where the microhabitat temperature lies in *both* predator and prey ranges. These times and temperatures are indicated in Figure 1. Including effects of both activity times in the functional response modifies (1) and leads to a temperature-mediated, *effective* number captured on day t as

$$(3) \quad n_c = kdA_s s_t \frac{N_t}{A},$$

where

$$(4) \quad s_t = \frac{1}{24} \text{meas} \left\{ \tau : \theta_l \leq \theta_m(t, \tau) \leq \theta_u, 0 \leq \tau \leq 24 \right\}$$

is the time that the microhabitat temperature is in the common zone Z . If there are P_t predators on day t , then the net *effective* number of captures is $kd(A_s/A)s_t N_t P_t$, measured in prey.

In this discussion we assigned no detection when prey are inactive. It is clear that this assumption can be modified to include situations where an active predator may accidentally encounter quiescent prey. Thus, gradations of the detection factor can be defined for different

zones, active predator-inactive prey, active prey-inactive predator, and so forth. In addition, in Figure 1 we have indicated a sinusoidal hourly temperature variation to avoid complexity in the model; but equally well a different temperature model, a stochastic model, or actual field data could be used.

The temperature-mediated functional response is part of an overall discrete growth model that includes a growth (or recruitment) rate $G_t(N_t)$, a natural mortality rate $M_t(N_t)$, and mortality due to predation. The natural mortality rate includes death caused by means other than predation; for example, in insects, sources of mortality may be pathogens (fungi, bacteria, etc.) or lack of fitness. In summary, the temperature-mediated dynamics is given by

$$(5) \quad N_{t+1} = N_t + G_t(N_t) - M_t(N_t) - kd(A_s/A)s_t N_t P_t, \quad t = 0, 1, 2, \dots,$$

where the initial prey population N_0 is prescribed. The model is nonautonomous because of the time dependence, and it is metered because the daily search time is computed on a faster time scale, namely, an hourly variation through equation (4).

As in all difference equations, e.g., (5) and the subsequent equations in this paper, the negative terms on the right side may become large and so the solution may not remain positive. To remedy this problem in (5), we set $N_{t+1} = 0$ when the right side is nonpositive. This corresponds to extinction of the prey.

We do not resolve predator dynamics, but rather we assume the predator population P_t is a prescribed input. For some systems, where the predator population is multiphagous, this may be a valid assumption. In mark-and-recapture experiments, Joern et al. [2006] found that lycosid spider populations were more or less constant over a summer season, as was their size distribution.

There are obvious effects that can be included to generalize this model. First, in more complex, structured environments, the microhabitat temperature may be a function of the ambient air temperature, which in turn may depend upon solar radiation, or sunlight, as well (Harrison and Fewell [1995]). Animals, for example insects or reptiles, may also thermoregulate in such environments, complicating the analysis; their body temperature may be the key to determining activity times. To avoid increasing complexity, we assume the body temperature, the microhabitat temperature, and the ambient air temperature

all coincide. Further, we have not included temperature dependence in the growth rate G_t or natural mortality rate M_t , although environmental changes can dramatically affect these rates. For example, an event like a hard freeze can have a catastrophic effect on survival of insect populations. We have not inserted prey behavioral characteristics in the model, such as prey vigilance, which can also alter its activity time and therefore its detection. Finally, as mentioned already, the daily, modified search time could also depend on other temperature zones where there are chance encounters between an inactive prey and an active predator; in (5) we include only an overlapping activity zone Z . We have made our assumptions so that the key idea of a temperature-mediated functional response is not drowned by complex generalizations that may be included later.

2.2. Type II response. Including predator handling time leads to a classic Holling Type II functional response (Holling [1965]). We begin, prior to considering temperature, with the expression (1) for the number of prey captured in time T_s . If T denotes the time available to the predator on day t , not all of it can be used for searching for prey; a portion is required for handling prey that are captured. Then $T_s = T - T_h$, where T_h is the total time required for manipulating and consuming prey. (Clearly, we may divide T into finer intervals that include other times, for example, the time spent pursuing prey, digesting the food items, resting, and so on.) Substituting into (1) gives

$$n_c = kdA_s(T - T_h) \frac{N_t}{A}.$$

We impose the standard assumption that T_h is proportional to the number of prey captured, or $T_h = hn_c$. Here, h is the time to handle a single prey, per predator. Substituting into the last expression and solving for n_c gives

$$n_c = \frac{kd(A_s/A)TN_t}{1 + kd(A_s/A)hN_t},$$

which is the number captured, or the predator's functional response. The dimensions are prey per predator, and the right side is the usual Type II response that saturates at the value $n_c = T/h$.

We can include temperature variation, as in the Type I response, by modifying the total time T . We replace T in the numerator

by the temperature dependent factor s_t , given in (4). Therefore, a temperature-mediated Type II response can be written

$$n_c = \frac{kd(A_s/A)s_tN_t}{1 + kd(A_s/A)hN_t} P_t,$$

which is the number captured on day t by P_t predators. The corresponding temperature-mediated prey abundance is therefore given by the nonautonomous, metered model

$$(6) \quad N_{t+1} = N_t + G_t(N_t) - M_t(N_t) - \frac{kd(A_s/A)s_tN_t}{1 + kd(A_s/A)hN_t} P_t.$$

In this nonautonomous case, the temperature-dependent predation rate does not saturate at a constant value. If the handling time h is zero, then (6) reduces to (5). In the usual way, e.g., see Case [2000, p. 247], if we assume the detection rate is a linearly increasing function in N_t , or $d = \alpha N_t$, we obtain a temperature-mediated Type III, or sigmoidal, response.

Generalizations are possible in different directions. The handling time may be temperature dependent, as may be the search rate A_s . Further, there are other functional responses that may be considered. Gilioli et al. [2005] introduce a continuous model of the form

$$\frac{dN}{dt} = -\omega \left(1 - e^{-\alpha N/\omega} \right),$$

where N is the prey population, ω is the predator demand rate, and α represents the “search rate expressing prey availability in relation to predator attack.” Both ω and α in this model are taken to be linearly increasing functions of temperature determined by fitting data. This model is a modification of the temperature independent supply-demand response (Gutierrez et al. [1995]) response, notwithstanding the comments by Royama [1971, p. 55], who questions the derivation of the response and has shown that it amounts to a simpler Ivlev response.

3. Applicability and simulations. In this section we discuss the types of trophic interactions that may be modeled by (5) or (6), and we carry out simulations for a model interaction between a poikilothermic

predator and a small mammal. The focus is on terrestrial, rather than marine interactions.

Variable environmental temperature levels more strongly affect poikilothermic animals (arthropods, reptiles, and so on) than endothermic animals, and these effects are translated to their interactions. As a consequence, activity times will be altered more strongly for poikilothermic predators or prey. For example, in reptile predation of small mammals, temperature variations may significantly change the activity period of the reptile, but the mammal may continue activity as usual. For grasshoppers, bird predators may experience little, if any, change in their search times during a cold period, while grasshoppers will be inactive and may be undetectable by the birds. The interaction between two arthropods, for example, a spider and an insect, may be strongly affected by changes in activity times for both.

There is a limitation of the model, as it stands, for poikilothermic prey. Because development rates for many of these animals are so strongly temperature dependent, growth rates almost certainly contain temperature dependence, and therefore the time horizon for passage to adult is not constant. One must carefully consider the life history of such animals in developing the temperature-dependent models. For example, adult grasshoppers in many temperate climate zones lay eggs in the late summer and fall; the eggs "over-winter," hatching in the late spring. The cohorts of young nymphs then pass through well-defined instars to reach adulthood, and the nymphal period varies considerably with temperature. Typically, we would not model populations of nymphal grasshoppers during a seasonal developmental period which includes recruitment G_t . However, models (5) and (6) could apply to an adult population over several days in the late summer with $G_t > 0$ being the recruitment of new adults, i.e., those adults graduating from the final instar, over that time period. In this case the model takes the form

$$(7) \quad N_{t+1} = N_t + G_t - mN_t - \frac{kd(A_s/A)s_tN_t}{1 + kd(A_s/A)hN_t} P_t,$$

where G_t is the recruitment rate of adults, and m is a daily, natural mortality rate. The model can be altered to include populations of nymphs if the rate of development, which is temperature dependent, is included, resulting in a physiologically structured model with time

evolving at the development rate, say, degree-days per day, see Logan et al. [2007].

Reptiles and small mammals, e.g., snakes and voles, provide a different example. In this interaction, temperature may strongly affect the poikilothermic predator by altering its search time. Growth and mortality rates in the prey population can be included if the time scale for growth is not too long compared to the time scale for predation events. This brings up the issue of time scales. Predation events that depend upon temperature variation often occur on a short time scale, say a day, while prey growth rates may be on the order of months or longer. The dynamics of these interactions is inherently multi-scaled. The metered model calculates predation on the scale of days. One may be able to scale up to longer time periods, say years, by an averaging or homogenization process.

To illustrate the model we consider an endothermic prey population that grows logistically, with a Type II predator functional response. The prey are assumed to be active under all temperature regimes, while the predator is poikilothermic and subject to variations in the time it has available for searching. Therefore, referring to Figure 1, the prey zone consists of all temperatures and the predator zone coincides with the common activity zone. Thus, $s_t = 1/24 \text{meas} \{ \tau : \theta_l^{\text{pred}} \leq \theta_m(t, \tau) \leq \theta_u^{\text{pred}}, 0 \leq \tau \leq 24 \}$. The model is

$$(8) \quad N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K} \right) - \frac{kd(A_s/A)s_tN_t}{1 + kd(A_s/A)hN_t} P_t,$$

where K is the carrying capacity of the prey, r is its intrinsic growth rate, and P_t is the population of a predator. Because we assume the prey are active at all times, the detection rate is constant. We assume $P_t = P = \text{const}$. The discrete logistics equation exhibits period doubling bifurcations in the parameter r , leading to chaotic dynamics, e.g., see Kot [2001]. Sample values of r give: $r = 0.01$, (monotonic increase to carrying capacity), $r = 1.9$ (damped oscillations about the carrying capacity), $r = 2.2$ (2-cycles), $r = 2.5$ (4-cycles) and $r = 2.55$ (8-cycles). For $r \approx 2.5699$ the solution behavior becomes chaotic. Therefore, we expect different dynamics for different values of the growth rate. Our simulations use $r = 0.02$, which is a growth rate that may correspond to a small rodent, e.g., a vole. For larger values of r , growth dominates the dynamics and brings to the forefront complications with multiple time scales.

Other approaches are possible as well. In place of the logistics growth model equation in (8), one could equally use a Ricker or a Beverton-Holt growth model, see Gurney and Nisbet [1998, p. 125] for the definitions and derivations. An example of this approach is the classical elk-wolf model that uses a Ricker growth model and a type 3 functional response, Dixon et al. [1997]. Alternately, one could reformulate the model using only a Ricker model, or Beverton-Holt, and reconstruct the temperature-dependent predation effects as part of the survivorship factors, or parameters, in the model. Although this method eliminates the possibility of obtaining negative population values, it leads to less intuitive and more *ad hoc* assumptions about where to put the temperature dependence. Therefore, we use (8) with the stipulation that $N_t = 0$ (extinction) whenever the right side evaluates to negative or a negative value.

The goal is to simulate the effects of temperature variation, and thus we fix values of the following population parameters:

$$(9) \quad \begin{aligned} A &= 250,000, & A_s &= 2500, & K &= 2500, \\ r &= 0.02, & k &= 0.5, & d &= 0.75, \\ h &= 5, & P &= 250, & N_0 &= 2000. \end{aligned}$$

We will vary parameters that govern the temperature history.

The temperature input to the model is stochastic. We take the average daily temperature over one year to be a simple periodic function

$$\theta_t^{\text{avg}} = \theta^* - a \cos\left(\frac{2\pi}{365}(35 - t)\right),$$

where t is the Julian day of the year, θ^* is the average yearly temperature and a is the yearly amplitude. Then we define the stochastic, daily average temperature by the first-order autoregressive process, e.g., see Brown and Rothery [1993, p. 505],

$$(10) \quad \Theta_{t+1} = \theta_t^{\text{avg}} + \alpha(\Theta_t - \theta_t^{\text{avg}}) + \sigma_1 \sqrt{1 - \alpha^2} Z,$$

where α is the autocorrelation, σ_1 is the standard deviation and Z is normal random variable with zero mean and unit variance. We generate the temperature amplitude each day via the autoregression process

$$A_{t+1} = a + \beta(A_t - a) + \sigma_2 \sqrt{1 - \beta^2} Z,$$

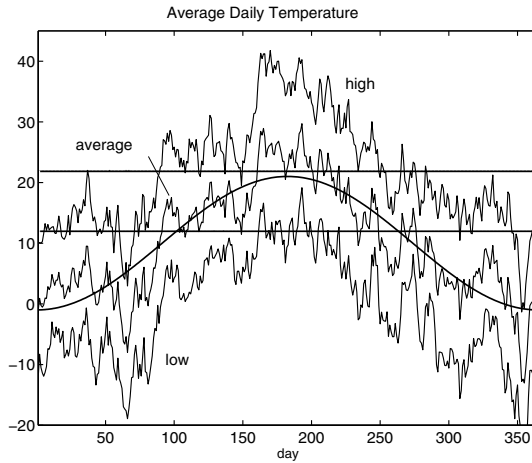


FIGURE 2. A realization of the average daily temperature over a year (the middle process lying between the high and low averages). The solid curve models the average daily temperature, and the temperature interval between the two horizontal lines, $\theta_l^{\text{pred}} = 12^\circ$ and $\theta_u^{\text{pred}} = 22^\circ$, represent the predator activity zone. The physical and stochastic temperature parameters, which are defined in the text, are: $a = 11$, $\theta^* = 10$, $\alpha = 0.9$, $\beta = 0.8$, $\sigma_1 = 4.4$, $\sigma_2 = 1.5$.

where β is the autocorrelation and σ_2 is the standard deviation. Figure 2 shows a stochastic realization of the average temperature variation Θ_t along with the average high and low, $\Theta_t \pm A_t$. Finally, the actual hourly temperature on day t is

$$\Theta_{t+1,\tau} = \Theta_t - A_t \cos\left(\frac{\pi}{12} \tau\right), \quad \tau = 0, 1, 2, \dots, 24.$$

As remarked earlier, to avoid complications with the physical structure of the environment and issues with predator thermoregulation, we take the microhabitat temperature $\theta_m(t, \tau)$ in the definition of the search time s_t to be equal to the ambient air temperature. Thus,

$$s_t = \frac{1}{24} \text{meas} \left\{ \tau : \theta_l^{\text{pred}} \leq \Theta_{t+1,\tau} \leq \theta_u^{\text{pred}}, \quad 0 \leq \tau \leq 24 \right\}.$$

Hence, all of the temperatures parameters will affect the calculation of the search time. We do not embark on a complete parameter study, but rather investigate the effects of amplitude, which measures variability, and mean temperature, which measures the level.

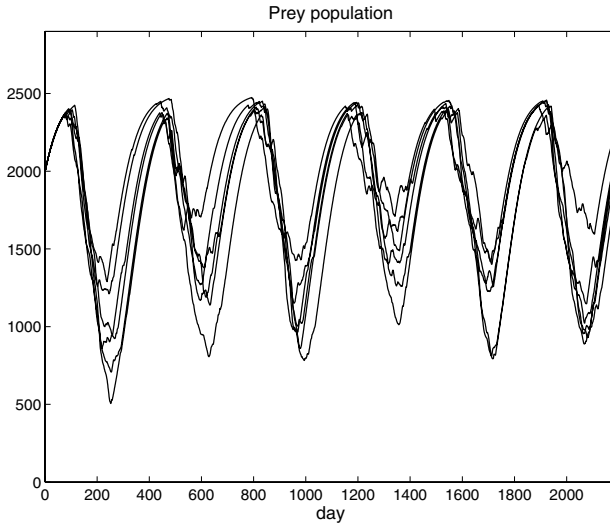


FIGURE 3. Baseline simulation of six realizations of the population over six years with parameters given by (9) and (11).

The baseline temperature values for the benchmark run are:

$$(11) \quad \theta^* = 10, \quad a = 11, \quad \alpha = 0.9, \quad \sigma_1 = 4.4, \quad \beta = 0.9, \quad \sigma_2 = 4.4.$$

Figure 3 shows six realizations of the prey population over a six-year period using the baseline parameter values (9) and (11). The population oscillates with dips in hotter summer temperatures, where predation is higher, and recovery when the temperature gets colder. Temperature variation is driving the dynamics. If temperature effects were not included, the population would monotonically approach a stable carrying capacity less than K , because of the predation effect. If environmental stochasticity were included by adding noise to the deterministic model (on a log scale), a still different picture would emerge showing random fluctuations about a mean population.

Figure 4 illustrates the effect of raising the average temperature two degrees, from $\theta^* = 10$ to $\theta^* = 12$. It shows increasing oscillations with extinctions occurring. Increasing the average temperature still further accentuates this effect, leading to extinction in most cases. Lowering the average temperature from its baseline value (simulations not shown)

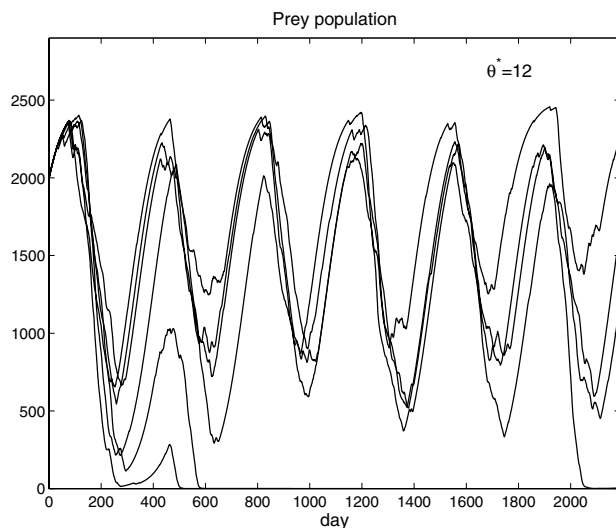


FIGURE 4. Population simulations over six years with average daily temperature $\theta^* = 12$, or two degrees above the baseline value. The remaining parameters are given by (9) and (11).

is beneficial to the prey, and the prey abundance remains near carrying capacity with small amplitude dips during the hotter seasons.

Figures 5 and 6 show effects of increasing and decreasing the average temperature *amplitude* a , respectively. An increase in a leads to increased oscillations and extinctions, while lowering amplitudes leads to populations near carrying capacity with small dips during the summer seasons. The conclusion is, in this system, increased fluctuations in temperatures are detrimental to the prey and can cause decreased populations or extinction.

Figures 7 and 8 show the results of changing statistical parameters in the autocorrelation relation (10) that defines the temperature history. Increasing the variability σ_1 from 4.4 to 6.4 causes the amplitude of the oscillations of prey abundance to increase, which can lead to extinction, Figure 7; decreasing σ_1 stabilizes the oscillations, and the profiles are similar to the baseline simulation shown in Figure 3. Increasing the autocorrelation coefficient α from 0.90 to 0.96 causes some increase in the amplitudes of the population, leading to extinction for some realizations, Figure 8. We expect, e.g., see Smith [1974], that as the

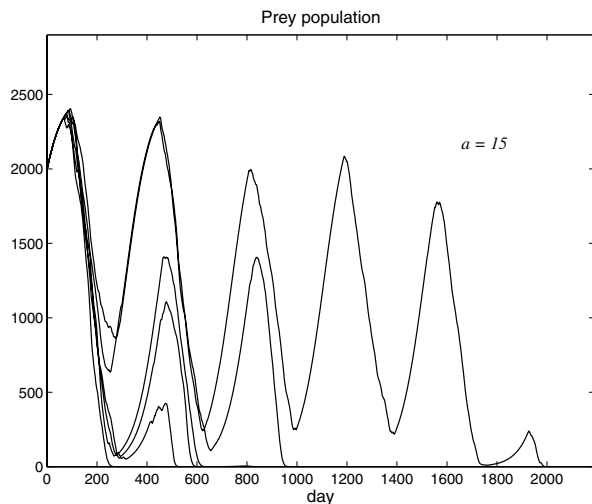


FIGURE 5. Population simulations over six years with average yearly amplitude $a = 15$, which is four degrees above its baseline value. The remaining parameters are given by (9) and (11).

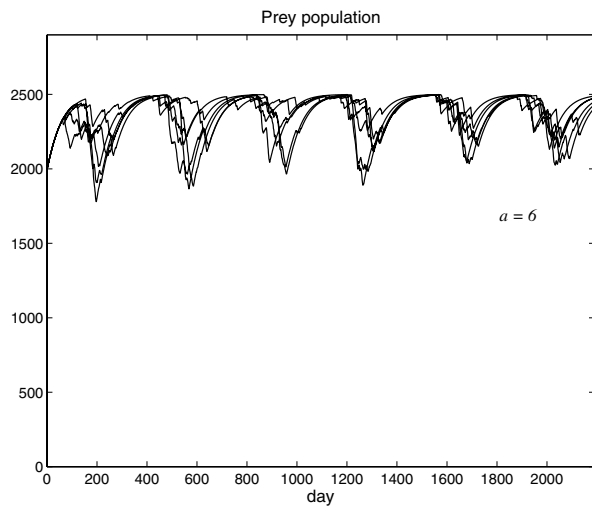


FIGURE 6. Population simulations over six years with average yearly amplitude $a = 6$, or four degrees below its baseline value. The remaining parameters are given by (9) and (11).

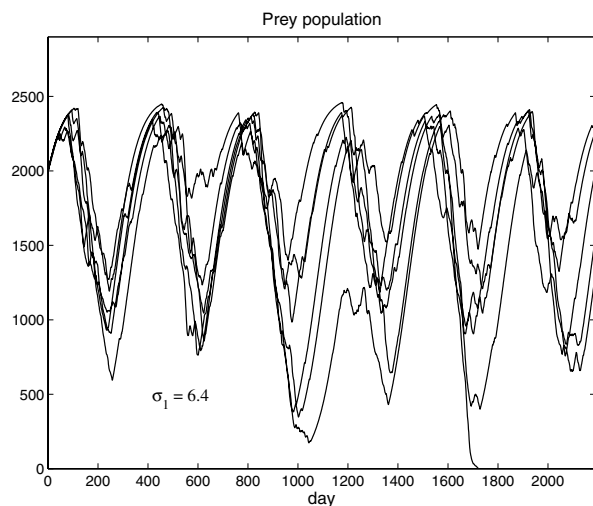


FIGURE 7. Population simulations over six years with $\sigma_1 = 6.4$. This increases the measure of the variability of the temperature over its baseline value of $\sigma_1 = 4.4$. The remaining parameters are given by (9) and (11).

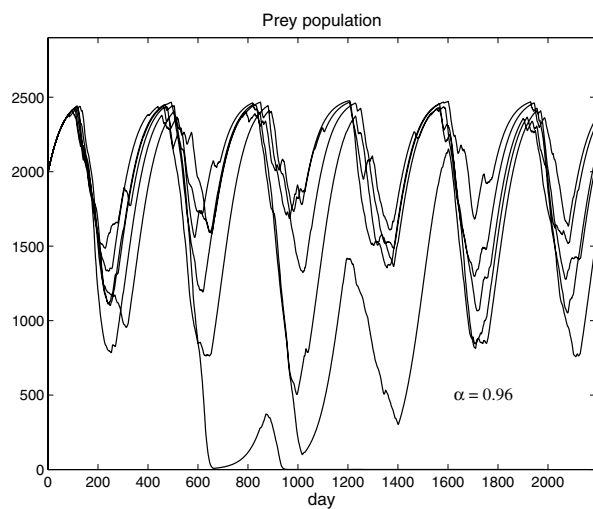


FIGURE 8. Population simulations over six years with $\alpha = 0.96$. The remaining parameters are given by (9) and (11).

variance of the temperature input parameters becomes large compared to the time scale of the dynamics, the oscillations will increase thereby leading to more extinctions. This is confirmed by the simulations.

We observe from Figure 8 that the prey go to extinction in one of the realizations. In a large number of realizations (1000), with the parameters given as in Figure 8, we find that the prey become extinct in 5.2% of the runs. Figure 9 shows a histogram indicating the frequency of final prey abundance over the six-year period in 1000 runs. The mean of the distribution is 1842 and the standard deviation is 588. If the period increases from 6 to 24 years, then the mean drops to 1662 with standard deviation increasing to 718; over a 36-year period, the mean and standard deviation shift to 1480 and 971, respectively. Over long times (as $t \rightarrow \infty$) we expect the probability that the prey population becomes extinct will approach unity (Lewontin and Cohen [1969], May [1971]). This expectation is confirmed by the simulations. For the parameters given in Figure 8 and for 1000 simulations, if we increase the number of years from 6 to 24, then the percent extinctions increases from 5.2% to 15%; for 36-year simulations the percent extinctions rises to 28%. Over a 100-year period, almost all the prey realizations become extinct. As the number of years in the simulations increases from a small number to a large number, the shape of the distribution changes from one whose mode is at the right (up near carrying capacity), to one whose mode is at the left (near extinction).

Simulations (not shown) also indicate the behavior of the model when other parameters change. If the growth rate r of the prey is increased, then the population quickly adjusts and moves toward equilibrium, lessening the effect of the stochastic inputs; so growth dominates variability, indicating that a population can compensate for modest temperature change by increasing its growth. For larger r we observe that chaos dominates, which is expected because of the logistics map for growth; so, the chaotic regime is an artifact of the model. If the initial population is higher than carrying capacity (e.g., $K = 2500$, $N_0 = 3000$), then the population decreases to the equilibrium and a pattern of oscillation is set up similar to that shown in Figure 8.

Reasonably small changes in the number of predators has a strong effect on the model. If P is increased 20% from 250 (the baseline value in Figure 8) to 300, then the amplitude of oscillations increase dramatically and the population goes to extinction quickly. If P is

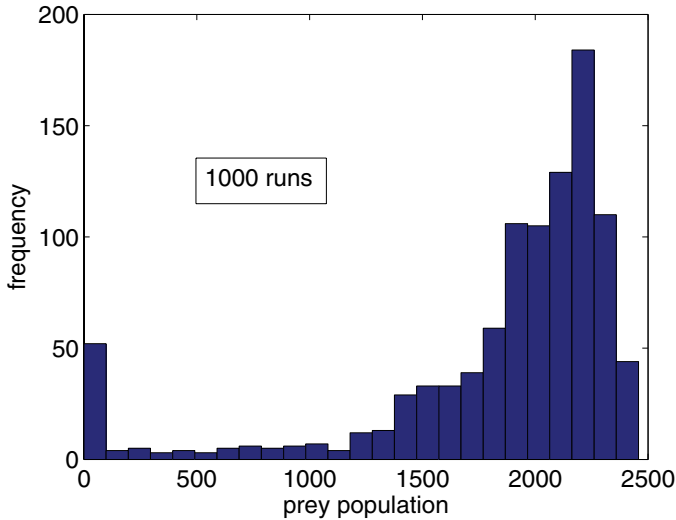


FIGURE 9. A histogram of final prey abundance over a six-year period using 1000 simulations. The parameters are the same as those from Figure 8. The mean is 1842 and the standard deviation is 588.

decreased to 200, then oscillations decrease and the population varies around the equilibrium. Note, from (8), that P occurs linearly in the predation term. Therefore, the same effects can be observed when similar changes are induced in the temperature dependent search time s_t , which also occurs linearly.

4. Summary. In standard predator-prey models, randomness can be included in the dynamics by introducing environmental or demographic stochasticity in a variety of ways, for example, by replacing a parameter with a random variable or adding noise to the parameters or to the dynamical equations themselves, or adding random effects on a logarithm or square-root scale. Temperature, as well as other abiotic factors, may be included in these general insertions with no rational relationship between the assumption of temperature dependence and the actual mechanism where it enters the model. In this paper we presented a simple, rational method to include time-dependent, temperature-mediated effects in standard predator functional responses in a specific, mechanistic manner with a direct ecological interpreta-

tion. The method involves modifications of the predator's search time by limiting factors determined by the fraction of the day that the temperature is within the predator's and prey's activity periods. The basic hypothesis is that temperature variations affect times when predation events can occur. This is especially true for poikilothermic animals. The model may be applicable to interactions where at least one of the constituents is poikilothermic and where growth rates and other dynamics are on the same time scale as variations in daily temperature. As we have presented it, the model is not applicable to prey whose development is strongly influenced by temperature, e.g., arthropods, unless we consider time periods when development is a nonissue, as in the adult stage. But, the model can be adapted to these cases if time proceeds at the speed of development. Although we focused on discrete time models, the idea and formulas are easily extended to continuous time interactions.

Temperature-independent models are complex because of the number of parameters involved in growth rates, mortality rates, and predation rates. When temperature variation is included, the complexity increases significantly because of the additional number of parameters required to define temperature histories. Further, stochasticity plays an essential role. A complete parameter study, which would be accompanied by large numbers of realizations and simulations to determine the effects of varying key temperature and other model parameters, seems untenable. Moreover, highly diverse interactions take place between various taxa, again leading to extensive model building. In reality, each case is a separate study. Therefore, in this brief communication, we have considered only a single, generic interaction where a temperature-mediated predation response was incorporated into a logistic growth model. This case illustrates a general method that may apply to specific populations through separate case studies and further research. Applications may also include control of temperatures in greenhouses to maximize biological control of insect pests.

The main conclusion in this work, interpreted in a context of global climate change, is that temperature amplitudes, which measure variability, and mean temperatures, which measure temperature levels, can affect survivorship in a significant way. Qualitatively, this inference is common knowledge, especially for the case of mean temperature levels. The mechanistic model we developed gives quantitative support on

which to base qualitative reasoning. Our model simulations show that variability plays an equal role with average temperature levels in modulating predation events, and uncertainty in temperature fluctuations, as measured by statistical properties of a temperature time series model, can further affect prey abundance, possibly leading to extinctions. The simulations also confirm theoretical results that have been obtained for simple models, namely, that increased temperature variability leads to increased oscillations and extinctions, with the probability of extinction approaching unity as time increases.

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