AN INDIVIDUAL, STOCHASTIC MODEL OF GROWTH INCORPORATING STATE-DEPENDENT RISK AND RANDOM FORAGING AND CLIMATE

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ABSTRACT. We model the effects of both stochastic and deterministic temperature variations on arthropod predator-prey systems. Specifically, we study the stochastic dynamics of arthropod predator-prey interactions under a varying temperature regime, and we develop an individual model of a prey under pressure from a predator, with vigilance (or foraging effort), search rates, attack rates, and other predation parameters dependent on daily temperature variations. Simulations suggest that an increase in the daily average temperature may benefit both predator and prey. Furthermore, simulations show that anti-predator behavior may indeed decrease predation but at the expense of reduced prey survivorship because of a greater increase in other types of mortality.

1. **Introduction.** A central issue in population ecology is to determine factors that regulate populations and trophic interactions (Kareiva et al. [27], Murdoch et al. [40], Joern et al. [25]). Environmental factors, many of which are stochastic, are foremost among mechanisms that affect the dynamics of ecosystems. In particular, temperature variations have a strong influence on arthropod populations and their interactions (Logan & Powell [34], Logan & Bentz [33], Gilbert & Ragworth [14], Bentz et al. [5]). In an era when global climate change is a major issue, understanding the effects of these variations on resource-consumer dynamics is essential (see Burns [8] for a bibliography; Joern et al. [25], Belovsky & Joern [2]). The key ideas underlying arthropod predator-prey interactions are put forth in Hassell [19] and also reviewed, for example, in Murdoch et al. [40]). However, with few exceptions (Mack & Smilowitz [38], Gilioli et al. [15], Logan et al. [36]), the inclusion of temperature in many of the ecological models addressing predator-prey relationships seems to be lacking. In brief, in this paper we study the stochastic dynamics of arthropod predator-prey interactions under a varying temperature regime, and we develop an individual model of a host under pressure from a predator, with vigilance (or foraging effort), search rates, attack rates, and other predation parameters dependent upon daily temperature variations.

Our model is motivated by recent work by Luttbeg et al. [37], who study trait- and density-mediated effects in a foraging-predation risk environment. They model foraging success as a binomial random variable depending upon the foraging effort and resource level. The foraging effort can be interpreted as prey vigilance, and it depends upon predation risk. In our model the predation risk is a function of the state, or fitness, of the prey, the prey's vigilance, and the predator density. In Luttbeg et al. [37] and in our model, the prey's state evolves over a fixed time horizon by accumulating, each day, the difference between foraging success (intake) that day and a constant daily metabolic cost. No effort is made in our model to resolve predator population dynamics. We assume that predator density is an input, determined, for example, from field estimates. In summary, we extend Luttbeg et al. [37] to include

- temperature effects,
- foraging success dependent upon nutritional state,
- nonlinear growth rate.

For poikilothermic organisms, daily activity is largely determined by temperature. Changes in temperature can alter the daily activities for both predator and prey, resulting in possible changes in predation and foraging rates. For example, in a predator-prey system where the predator and prey are active under different temperature ranges (e.g., wandering lycosid spiders and grasshoppers), an increase in the daily average temperature may prove beneficial to prey by providing additional foraging time in the absence of predators. This in turn may result in a higher prey nutritional state and provide prey with additional energy that may allow for increased anti-predator behavior and lower predation. The trade-off between foraging and predation risk is discussed in Brown et al. [7], Houston et al. [21], Houston & McNamara [20], and Lima & Bednekoff [31]. We add to this body of work by providing a functional form for vigilance that depends on temperature-dependent quantities, such as predator search rate, prey nutritional state, and the effective predator density (i.e., active predators).

The purpose of this paper is twofold: first to present a rational mechanism for the inclusion of temperature into predator-prey models for terrestrial ectotherms, and second to illustrate the model by applying it to an actual predator-prey system for wandering lycosid spiders and grasshoppers (Beckerman et al. [1], Danner & Joern [11], [12], [13], Joern et al. [24], Joern & Gaines [23], Logan et al. [36]). In addition, we perform simulations for both ignorant and non-ignorant prey (that employ vigilance) using three different average daily temperatures. We simulate the life history for 10,000 individual prey to determine prey survivorship, predation, total prey mortality, and adult prey mass. In particular, we use the simulations for the spider-grasshopper system to address the following questions: will an increase in daily average temperature prove favorable for the predator or prey (i.e., increased predation, or increased prey survivorship); will an increase in daily average temperature change adult mass; what is the trade-off between types of prey mortality when prey employ anti-predator behavior (i.e., will the survivorship gain from reduced predation offset the additional mortality that results from reduced foraging)?
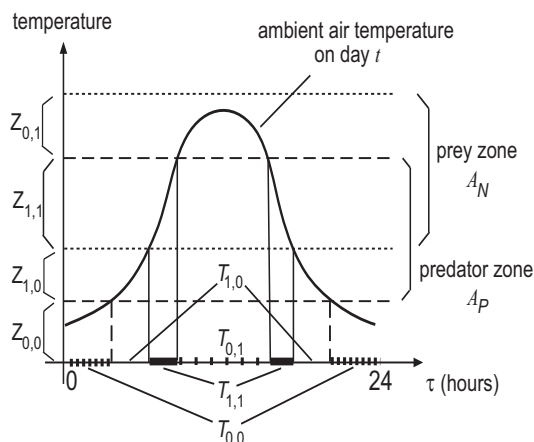
FIGURE 1. Depiction of hourly ambient air temperature. The various activity zones $(Z_{i,j})$ are shown on the vertical axis, and the corresponding measure of the time spent in these zones $(T_{i,j})$ is shown on the horizontal axis.

2. Model components.

2.1. **Temperature zones.** Insects are ectotherms and must rely on external heat sources and sinks to control body temperature. Thus, to adequately model predator-prey systems involving insects, it is essential to include the effects that ambient air temperature has on determining body temperature, as it influences both food acquisition and processing capabilities for ectotherms (Huey and Stevenson [22], Crowder & Magnuson [10], Karasov [26], Zimmerman & Tracy [52], Yang & Joern [50] [51], Harrison & Fewell [18]). For simplicity, we assume the microhabitat temperature coincides with the ambient air temperature, although we recognize that microhabitat temperature is actually a function of ambient air temperature and solar radiation falling on the environment. Further, many animals (ectotherms) exhibit behavior that allows them to thermoregulate in their environment. While we choose to ignore these factors in this work, the reader is referred to Logan et al. [36] for a model that relates microhabitat temperature to ambient air temperature and solar radiation. Temperature can further complicate ectotherm predator-prey interaction when the prey and predator possess differing temperature ranges in which they are effectively able to thermoregulate. For example, spiders exert a significant limiting influence on grasshopper populations through both direct effects, such as predation (Belovsky & Slade [3], Oedekoven & Joern [41], [42], and indirect effects, such as reduced foraging effort due to the presence of spiders (vigilance) (Rothley et al. [44], Danner & Joern [12]). The responses exhibited by both species are affected directly by temperature (Kemp [28], Li & Jackson [30], Lactin & Johnson [29]), with the daily activity schedule of spiders differing significantly from that of grasshoppers. Generally, spiders are active in an ambient air temperature zone

(A_P in Figure 1) that includes temperatures below those needed by grasshoppers to effectively thermal regulate, while grasshoppers are active in a range of temperatures (A_N) which include values higher than those at which spiders can effectively operate. Thus, to adequately model the daily dynamics of spider and grasshopper interactions, we define four "activity zones" (Figure 1). These zones are easily adapted to other predator-prey systems and the associated dynamics that occur in these zones is also highly species dependent.

The activity zone $Z_{1,1}$ is defined by the overlapping temperature zone in which both the predator and prey exhibit highly active behavior. Within this zone, we expect maximum interaction between the species with associated complex predation dynamics. For example, it is expected that predation is high in this zone when predators are highly dependent upon prey motion for identifying prey. At the same time, this activity zone will induce high sensory processing for prey, thus allowing prey with highly evolved anti-predator mechanisms potentially to elude predation, but at the expense of reduced foraging. The activity zone $Z_{1,0}$ is defined by temperatures that are conducive for active behavior in predators and inactive behavior by prey. The dynamics of predation in the zone greatly depend on the ability of the predator in identifying inactive prey. If the predator has well evolved searching skills that allow it to identify stationary prey, then a large amount of predation can occur in this zone. On the other hand, if prey identification depends largely on prey motion, then this zone will produce predation dynamics similar to the dynamics that occur when prey are exhibiting anti-predator behavior. The zone $Z_{0,1}$ is highly favorable for prey foraging because predation, as well as the threat of predation, is very low. For example, in grasshopper–wolf spider interactions, the wolf spiders are effectively absent from the field when temperatures are above those in their active temperature range, thus creating ideal foraging conditions for grasshoppers. Finally, in the zone $Z_{0,0}$, both the predator and prey are inactive, and little foraging or predation is occurring. For prey (or predators), extended time in this zone limits the time available to forage actively and thus increases risk of starvation.

These activity zones help explain temporal differences observed in many predator-prey interactions. We let $T_{i,j}(n)$ denote the time spent in activity zone $Z_{i,j}$ on day n. We assume that there are upper and lower temperature thresholds $\theta_{\min}$ and $\theta_{\max}$ between which both predator and prey are active. If $\theta(\tau, n)$ is the hourly temperature on day n where σ is measured in hours ($0 \leq \tau \leq 24$), then $T_{1,1}(n) = \mathrm{meas}\{\tau : \theta_{\min} \leq \theta(\tau, n) \leq \theta_{\max}\}$. Further, $T_{0,0} + T_{1,0} + T_{0,1} + T_{1,1} = 24$. Table 1 gives a summary of the activity zones.

Table 1. Activity zone behavior

Zone	Predator	Prey
$Z_{1,1}$	Active	Active
$Z_{1,0}$	Active	Inactive
$Z_{0,1}$	Inactive	Active
$Z_{0,0}$	Inactive	Inactive

For the simulations, we model the hourly ambient air temperature on day n by

$$\theta(\tau, n) = \overline{\theta}(n) + B \cos \frac{(\tau - 14)\pi}{12}, \quad 0 \leq \tau < 24, \qquad (2.1)$$

where $\overline{\theta}(n)$ is the average ambient air temperature on day n. The air temperature can also be obtained from field site data, but we take an average value compiled from the U.S. Weather Service [48] near a field site in western Nebraska. The average daily temperature on day n, computed over a 30-year period for the dates June 1 through September 30, can be fit by the quadratic

$$\overline{\theta}(n) = \theta_0 + 0.2547n - 0.0014n^2, \qquad (2.2)$$

where $\theta_0 = 17.01$ (Celsius) is the average temperature on June 1, with $R^2 = 0.96$. For simplicity we use an average daily amplitude of $B = 7.58$ degrees, but note that daily amplitude also varies with n.

2.2. **Fitness dynamics.** The costs and benefits of an action may depend on the state (fitness) of the animal. For small arthropods, such as insects, fitness varies on a daily, if not hourly, basis. For example, Simpson and Simpson [46] showed that nutrient titers in the hemolymph of grasshoppers change markedly within hours of consuming a meal. It was further observed that these nutrient titers play a significant role in triggering the onset of foraging (Simpson & Raubenheimer [45]). In this section we describe a measure for fitness and incorporate prey fitness into both the predation and foraging rates.

The rate at which prey accumulate mass is clearly prey specific. Moreover, the uniformity at which individuals within the same cohort grow is species dependent and varies with foraging success and food quality. For example, Chambers [9] observed that *Locusta migratoria* fed foods of various quality exhibit compensatory feeding and were able to defend a very tight range of mass targets and development rates. This contrasted strongly with the gypsy moth, *Lymantria dispar*, whose larvae (Stockhoff [47]) suffered marked differences in both pupal mass and development time when presented with food of variable quality. For the simulations and predictions included in this paper, we use a geometric model for mass growth, assuming adult prey mass differs by at most 10%, and we incorporate both prey growth rate and mass range in defining the daily fitness of prey.

To define prey fitness, we follow Luttbeg [37], but with significant refinements. To reflect the rapid changes in fitness that occur in small prey, we define daily fitness $s(n)$ by

$$s(n) = \left(\frac{m(n)}{m_{\text{mid}}(n)} \right)^{\kappa},$$

where $m(n)$ is the dry mass of the prey on day n and $m_{mid}(n)$ is the mid range value determined by the upper and lower growth curves on day n (Figure 2). The parameter κ determines the shape of the daily fitness curve. It is species dependent, and it depends on the role that fitness plays in determining foraging effort and prey vigilance. For example, when fitness is high ($s(n) > 1$), then prey can afford to be more vigilant (and thus reduce predation risk) than prey who are at a low level of fitness ($s(n) < 1$). The value of κ either increases or decreases the role that fitness plays in determining vigilance level or foraging effort. Further discussion on the role of κ is included in Section 2.4.

2.3. **Mass gain dynamics.** Using field data for hatch mass and adult mass (mg., dry weight) we follow Luttbeg [37] to create a mechanistic model for mass gain that is dependent upon the daily number of meals consumed. Additionally, we assume prey gain mass at a geometric rate until becoming adults (geometric growth occurs under the assumption of an energy budget model where both the rate of

consumption and the metabolic rate are proportional to mass (Gurney & Nisbet [17]). Our model is easily adapted to other mass gain rates, such as the linear model implicitly assumed in Luttbeg [37]. Furthermore, we employ a fixed time model (Houston & McNamara [20], Luttbeg [37]) that determines the length of the juvenile stage. That is, we assume that prey become adults in a fixed time horizon of 50 days (Luttbeg [37]). The model can be adapted to other approaches, such as a fixed-size horizon (prey become adults upon reaching a predetermined size range) (Houston & McNamara [20]).

For notation we use the double subscript i, j to denote dynamics that occur in activity zone $Z_{i,j}$. We assume that daily mass gain, $d_g(n)$, is determined by

$$d_g(n) = \begin{cases} -c_f + \left(\frac{\Delta_{\min}(n) + c_f}{x_{\min}} \right) x & \text{if } x \leq x_{\min} \\ \Delta_{\min}(n) + \left(\frac{\Delta_{\mathrm{mid}}(n) - \Delta_{\min}(n)}{x_{\mathrm{mid}} - x_{\min}} \right)(x - x_{\min}) & \text{if } x_{\min} < x \leq x_{\mathrm{mid}} \\ \Delta_{\mathrm{mid}}(n) + \left(\frac{\Delta_{\max}(n) - \Delta_{\mathrm{mid}}(n)}{x_{\max} - x_{\mathrm{mid}}} \right)(x - x_{\mathrm{mid}}) & \text{if } x_{\mathrm{mid}} < x \leq x_{\max} \\ \Delta_{\max}(n) & \text{if } x > x_{\max} \end{cases} \quad (2.3)$$

where $x(n)$ is the number of meals consumed on day n; c_f is a fixed daily metabolic cost; $x_{\min}$, x_{mid}, and $x_{\max}$ are the number of meals that result, respectively, in daily mass gains of $\Delta_{\min}(n)$, $\Delta_{\mathrm{mid}}(n)$, and $\Delta_{\max}(n)$. These mass gains correspond to the mass trajectories given in Figure 2.

Central to $d_g(n)$ is the daily meal consumption $x(n)$, which we assume is Poisson distributed. We let $X(n)$ be a random variable denoting the number of meals consumed by prey on day n. For arthropods, foraging behavior has been successfully modeled (Wolesensky et al. [49]) using the observation that time intervals between successive foraging events are exponentially distributed (Gross [16]). From this assumption it follows that the Poisson distribution is appropriate for the number of meals, $X_{i,j}$, consumed in the time interval $T_{i,j}$ with Poisson rate parameter $\lambda_{i,j} = \gamma_{ij}(1 - v_{ij})$. That is,

$$\Pr(X_{i,j}(n) = x_{i,j}(n)) \sim \mathrm{Poisson}(\lambda_{i,j} = \gamma_{ij}(1 - v_{ij})), \quad (2.4)$$

where $\gamma_{i,j}$ is the foraging rate (meals/hour) with no vigilance and $v_{i,j}$ is the level of vigilance exhibited by prey in zone $Z_{i,j}$ (vigilance is discussed in detail in the next section). Then

$$x(n) = \sum_{all \ i,j} x_{i,j}(n), \quad (2.5)$$

from which it follows that prey mass on day t is given by

$$m(n) = m(0) + \sum_{n=1}^{t} d_g(n),$$

where $m(0)$ is the initial prey mass. If, at any time, the prey mass on day n lies below the minimum mass trajectory on that day (lower curve in Figure 2), then we assume the prey dies due to starvation (or other natural causes).

2.4. **Predation and vigilance.** We assume that predation events occur according to a simple Poisson process (Lima & Bednekoff [31]) with attack rates

$$\alpha_{1,0}, \ \alpha_{0,1}, \ \alpha_{1,1}, \ \alpha_{0,0}$$

that differ according to the activity levels of the predator and prey. When modeling predation as a Poisson process, it is standard to include predator density, vigilance, and attack rate in the Poisson rate parameter ρ. In our model, we assume that this
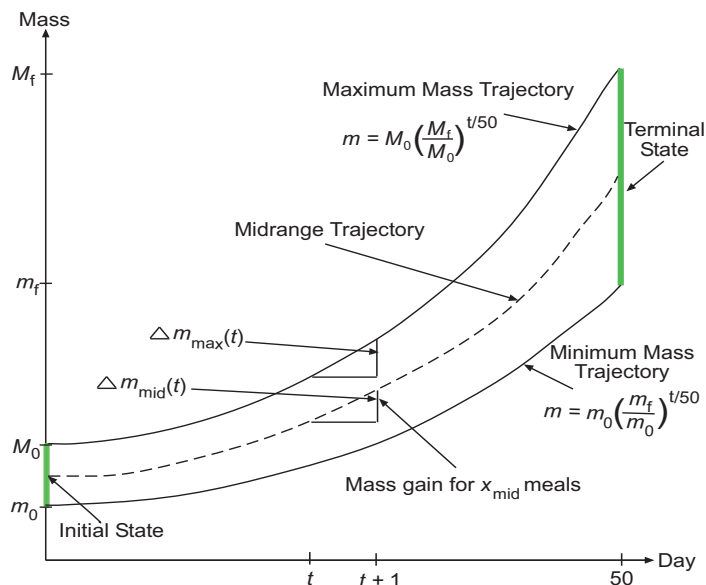
FIGURE 2. Schematic showing the maximum, minimum, and midrange mass trajectories over the 50-day nymphal period. The actual mass history of an individual lies in the band.

parameter varies according to the activity zone to which it corresponds. That is, $\rho_{i,j} = \rho_{i,j}(P_e, v_{i,j}, \alpha_{i,j})$, where P_e is the *effective* predator density and $v_{i,j}$ is the level of vigilance. The actual predator density P_a is fixed, as is the case for the rangeland grasshopper-lycosid system considered here (Joern et al. [24]). While the actual density of predators is assumed constant, the *effective* density of the predators depends on the various activity zones. For example, in temperature zones where the predator is active ($Z_{1,0}$, $Z_{1,1}$), we use density P_a, but in temperature zones where the predator is relatively inactive ($Z_{0,1}$, $Z_{0,0}$), we assume an effective density $P_e = \delta P_a$ with $0 \leq \delta \leq 1$. The value of δ reflects the severity of activity limitation that predators exhibit when encountering less than ideal temperatures. More precisely,

$$P_e = \begin{cases} P_a & \text{in } Z_{1,0} \text{ and } Z_{1,1} \\ \delta P_a & \text{in } Z_{0,1} \text{ and } Z_{0,0} \end{cases} . \tag{2.6}$$

The success of predators in securing prey depends in large part on the anti-predator behavior (vigilance) exhibited by the prey. While most models that incorporate vigilance (or feeding effort) are concerned with the level of vigilance that optimizes some fitness criteria (Houston et al. [21], Brown et al. [7], Lima & Bednekoff [31], Luttbeg et al. [37]), we include vigilance $v(t)$ in our model using an explanatory approach. That is, because vigilance is an anti-predator behavior of the prey, it should depend on prey traits (Lima & Steury [32]) such as fitness (nutritional state) and sensory characteristics, as well as predator density and predator activity (search speed). We state this mathematically by $v(t) = v(s, D, P_e, r_{i,j})$, where s is the nutritional state of the prey, D is the *sensory diameter* of the prey, P_e the effective density of the predator, and $r_{i,j}$ the search speed of the predator

(distance/predator/time) while in activity zone $Z_{i,j}$. The sensory diameter D is a measure of the region around prey in which they are able to perceive predation risk by using some type of sensory mode (e.g., visual, chemical, auditory, etc.). The value of D depends greatly on the complexity and structure of the habitat, and one expects the value of D to significantly influence prey survivorship. A small D is indicative of prey that are largely ignorant of predators and who would spend little time being vigilant, thereby leading to both increased foraging and increased predation. Large D refers to fretful prey that spend a large portion of time being vigilant at the expense of foraging. We determine the proportion of time that a prey spends being vigilant while in activity zone $Z_{i,j}$ by the dimensionless quantity

$$v_{i,j}(n) = \min\{\rho s(n)Dr_{i,j}P_e,\ 1\}. \tag{2.7}$$

The first term in braces is the proportion of time spent being vigilant. The probability of surviving predation on day t is determined by

$$\Pr(\text{survival}) = \prod_{\text{all } i,j} \exp(-\alpha_{i,j}(1 - v_{i,j})^2 T_{i,j}). \tag{2.8}$$

To make (2.7) dimensionless we multiply by the factor ρ, which we give value unity and dimension time. In general, it is expected that prey with a high level of fitness ($s(n) > 1$) can afford to be more vigilant than prey with a low level of fitness ($s(n) < 1$). The exact role that fitness plays in determining vigilance depends on the parameter κ used in defining the daily fitness $s(n)$. If fitness exerts a large influence on vigilance, then a large κ should be used, whereas if fitness plays a small role in determining vigilance, then κ near 0 would be appropriate.

We now summarize the algorithm used in the simulations. We track the daily mass increase and the total mortality for 10,000 individual prey in a cohort over their nymphal period. For an individual with initial mass $m(0)$, the mass gain, survivorship, and mortality (from both starvation and predation) are computed recursively, day to day. Specifically, on a given day, the times $T_{i,j}$ (representing the measure of the time spent in temperature zone $Z_{i,j}$) are calculated from the daily hourly temperature profile. Using a Poisson random variable (2.4), this determines the number of meals (2.5), which determines the daily mass gain d_g (2.3) on day n, and hence the natural survivorship. On the same day, the probability of surviving predation is determined from (2.8). This information is then used as the initial conditions for the next day.

3. **Simulations and results.** While we recognize that predator-prey systems are complex with subtle nuances, simulations using our stochastic model provide opportunities to investigate, at least qualitatively, ecological questions involving temperature modulation within a predator-prey system. In particular, we examine how changes in temperature affect

1. survivorship through changes in predation and other mortality,
2. adult fitness (or mass) of prey upon reaching adulthood, and
3. anti-predator behavior, such as vigilance.

Table 2 provides a listing of the primary model components, parameters, and functions used in the simulations. The parameter values reflect grasshopper-spider interactions in a grassland ecosystem where field experiments show that spider densities and size distributions are nearly constant (Joern et al. [24]). The initial simulations use a deterministic temperature ((2.1), (2.2)) and assume ignorant prey (i.e., no vigilance). These baseline results are later compared to simulations

assuming non-ignorant prey and simulations that employ a stochastic daily average temperature. In all cases, the plots and analysis reflect typical realizations resulting from 10,000 individual runs.

Table 2. Primary model components, parameters, and functions.

Symbol	Definition	Additional Information	Units
$Z_{i,j}$	Activity zone	Temperature Dependent	
$T_{i,j}(n)$	Time spent in $Z_{i,j}$	Temperature Dependent	Hours
$m(n)$	Dry mass of prey	Used to define fitness	Mass
$m_{\mathrm{mid}}(n)$	Midrange prey mass	See growth curves	Mass
$s(n)$	Daily fitness	$s(n) = (m(n)/m_{\mathrm{mid}}(t))^{\kappa}$	
κ	Defines shape of $s(n)$	$\kappa = 1$	
$d_g(n)$	Daily mass gain	Meal dependent	Mass
c_f	Daily Maintenance	$c_f = 2$	Mass
$x(n)$	Prey meals on day n	Determines growth	Meals
$f_1(x)$	Mass gain function	see (2.3)	
$f_2(x)$	Mass gain function	see (2.3)	
$f_3(x)$	Mass gain function	see (2.3)	
x_{min}	Meals = Δ_{min}	$x_{\mathrm{min}} = 9$	Meals
x_{mid}	Meals = Δ_{mid}	$x_{\mathrm{mid}} = 12$	Meals
x_{max}	Meals = Δ_{max}	$x_{\mathrm{max}} = 15$	Meals
m_0	Minimum initial mass	$m_0 = 7$	Mass
M_0	Maximum initial mass	$M_0 = 9$	Mass
m_f	Minimum terminal mass	$m_f = 180$ mg.	Mass
M_f	Maximum terminal mass	$M_f = 200$ mg.	Mass
$\gamma_{i,j}$	Foraging w/o vigilance	$\gamma_{i,1} = 2/3$, $\gamma_{i,0} = 1/12$	$\frac{\text{Meals}}{\text{Hr}}$
$\alpha_{i,j}$	Attack rate	$\alpha_{1,1} = .005$, $\alpha_{1,0} = .0001$, $\alpha_{0,j} = 0$	per Hr
P_a	Actual predator density	$P_a = .01$	$\frac{\text{Pred}}{\text{Meter}^2}$
δ	Density parameter	$\delta = .05$	
P_e	Effective density	see (2.6)	$\frac{\text{Pred}}{\text{Meter}^2}$
$v(t)$	Vigilance	$0 \leq v(t) \leq 1$	
D	Sensory diameter	$D = 1$	Meter
$r_{i,j}$	Predator search rate	$r_{1,j} = 10$, $r_{0,j} = 0$	$\frac{\text{Meter}}{\text{Pred}\cdot\text{Hr}}$

3.1. **Baseline simulations: No vigilance.** Figure 3 shows survivorship (subplots (a), (b), (c)), predation (subplots (d), (e), (f)), and other mortality (subplots (g), (h), (i)) under a deterministic average daily temperature given by (2). The columns in Figure 3 correspond to letting T_0 in equation (2.2) equal $17.01°$ C, $17.51°$ C, and $18.01°$ C, respectively (i.e., changing the average daily temperature by 0.5 and 1 degree Celsius). Table 3 includes data related to Figure 3 and the relative percent changes over the time horizon that occur as the average temperature increases.

Table 3. Relative percent change with increasing temperature (no vigilance)

End of season results	Temperature constant T_0				
	$17.01°$	$17.51°$	% Change	$18.01°$	% Change
Survivorship	3.0%	5.0%	+66.67	7.70%	+54.0
Predation	15.09%	18.94%	+25.51	24.33%	+28.46
Starvation	81.91%	76.06%	−7.14	67.91%	−10.72
Mean Adult Mass (mg.)	191.29	191.59	+0.16	192.37	+0.41

As the average temperature increases, there is a corresponding increase in end-of-season survivorship, as illustrated in subplots (a), (b), and (c) of Figure 3 and row 2 of Table 3. This increase occurs despite a significant increase in predation (see subplots (e), (f), (g) of Figure 3 and row 3 of Table 3). The increase in predation is explained by additional predation occurring late in the growing season, due to greater survivorship. In all three predation subplots, the predation occurring in the first quarter of the growing season is approximately the same, but in subplots (e) and (f) greater predation can be observed in the latter part of the growing season. The results in Figure 3 are consistent with size-independent predation and prey with no resource (food) limitation. If size-dependent predation were included in the model, then the increased predation predicted later in the season would disappear, and the results would show an even greater increase in survivorship. For prey with resource limitations, the predicted increase in survivorship would be greatly reduced by additional mortality occurring later in the growing season. Subplots (h), (i), (j) of Figure 3 show predicted mortality caused by starvation, which in the model occurs when prey mass falls below the minimum mass trajectory (Figure 2). Prey mass in the model depends on meals ingested (foraging success) and will fall below the minimum mass trajectory when prey fail to consume sufficiently many daily meals (equation (2.5)). Our model corresponds to prey that hatch in the spring and mature through the summer; thus, the part of the day that is favorable for prey foraging increases throughout the growing season. Therefore, the probability that prey ingest sufficient meals to remain above the lower mass trajectory increases and hence lowers mortality caused by starvation later in the growing season. This trend is apparent in all three subplots ((h), (i), (j) of Figure 3) and agrees with empirical results for grasshoppers where death from starvation is more likely in young nymphs (Belovsky & Slade [4]).

3.2. **Non-ignorant prey: The cost of vigilance.** Figure 4 and Table 4 give results of simulations that include prey vigilance (equation(2.7)), while using the same temperature conditions as in 3.1. Subplots (a), (b), and (c) of Figure 4 still show an increase in survivorship with an increase in daily average temperature, but end-of-season survivorship is significantly lower than when vigilance is absent (subplots (a), (b), and (c) of Figure 3 and row 1 of Table 3). The effectiveness of vigilance in reducing predation is evident when comparing subplots (d), (e), and (f) of Figure 4 with the corresponding subplots in Figure 3. We see greater mortality occurring from starvation when vigilance is included (compare subplots (g), (h), (i) of Figure 4 to corresponding subplots in Figure 3). This increase in starvation results from prey spending a proportion of their day being vigilant, thus reducing their foraging success. Overall, the additional loss in survivorship that occurs from an increase in starvation more than offsets the gain in survivorship from reduced predation (compare subplots (a), (b), and (c) in Figure 4 with corresponding subplots in Figure 3). We call this loss in survivorship the *cost of vigilance*. An additional consequence of including vigilance is that the mean adult mass (hence adult fitness) of the prey (row 5 in Tables 3 and 4) tends to be slightly lower. This could have reproductive consequences and hence consequences on yearly prey dynamics, particularly if reproduction capacity (egg clutch size, for example) is mass dependent. In general, most models that include vigilance or feeding effort seek to determine an optimal level that maximizes some fitness criteria (examples include Lima & Bednekoff [31], Luttbeg et al. [37], McNamara & Houston [39], Brown [6], Brown et al. [7], Houston et al. [21]). That is not our goal. Instead, we model
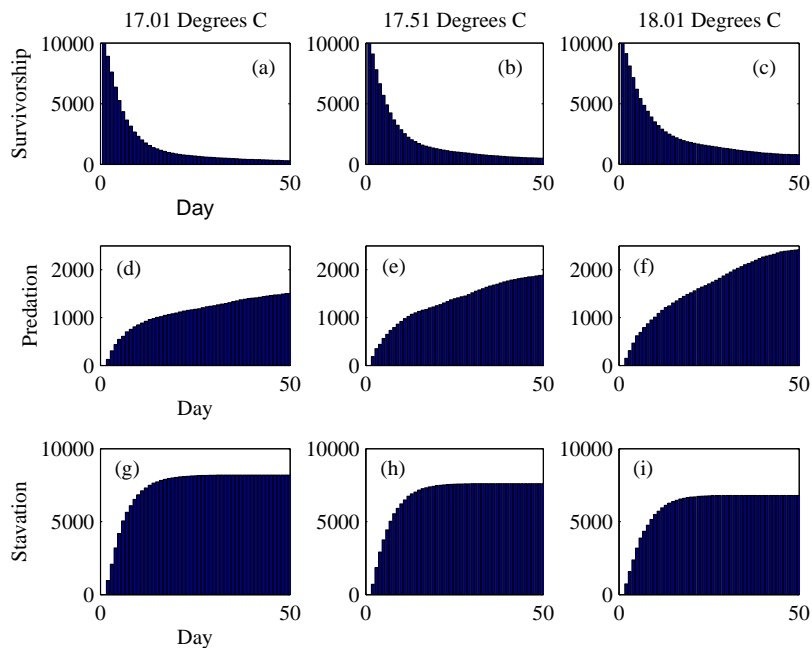
FIGURE 3. Baseline results. These subplots show results obtained by tracking 10,000 individual ignorant prey (no vigilance included) from a single cohort using a deterministic daily average temperature (equation (2.2)). The rows show survivorship, predation, and mortality from causes other than predation. The columns were obtained using 17.01° C, 17.51° C, and 18.01° C, respectively, for the average daily temperature (T_0 in equation (2.2))

the inclusion of a rational mechanism for individual prey vigilance and its effect on overall population survivorship.

Table 4. Relative percent change with increasing temperature (with vigilance)

End of season results	Temperature constant T_0				
	17.01°	17.51°	% Change	18.01°	% Change
Survivorship	1.09%	2.02%	+85.32	4.25%	+110.40
Predation	7.64%	10.22%	+33.77	12.91%	+26.32
Starvation	91.27%	87.76%	−3.85	82.84%	−5.61
Mean Adult Mass (mg.)	190.22	190.14	−0.04	191.31	+0.62

3.3. **Stochastic daily average temperature.** One motivation for this work is to show that small changes in temperature can have profound effects on predation and survivorship in predator-prey systems. In Sections 3.1 and 3.2 we investigated the effect of changing the daily average temperature in a deterministic temperature model. While much can be gained from such investigations, weather events that occur on the scale of days can severely limit prey foraging and predation events to the extent that, over the period of a few days, little or no foraging or predation may occur. To examine the ways weather events translate into survivorship and
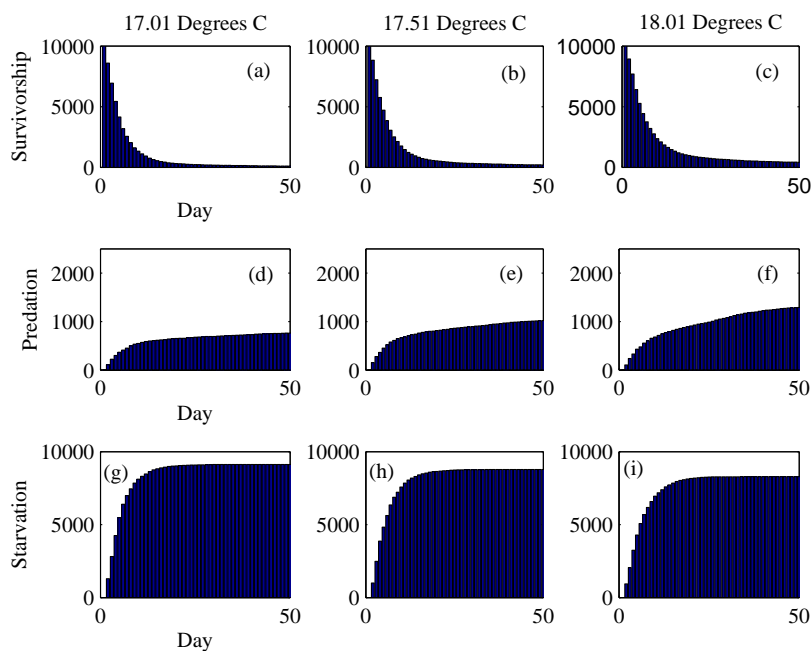
FIGURE 4. These subplots show results obtained by tracking 10,000 individual non-ignorant prey (vigilance is included) from a single cohort using a deterministic daily average temperature (equation (2.2)). The rows show survivorship, predation, and mortality from causes other than predation. The columns were obtained using 17.01° C, 17.51° C, and 18.01° C, respectively, for the average daily temperature (T_0) in equation (2.2)).

predation, we assume the temperature history (2.1) includes a stochastic average daily temperature input. That is, we replace $\overline{\theta}(n)$ in (2.1) by $\Theta(n)$, which we define by the first-order autoregressive process

$$\Theta(n+1) = \overline{\theta}(n) + \alpha(\Theta(n) - \overline{\theta}(n)) + \sigma\sqrt{1 - \upsilon^2}Z, \qquad (3.9)$$

where α is the autocorrelation, σ is the standard deviation, and Z is a normal random variable with zero mean and unit variance. Figure 5 gives a seasonal realization of the average daily temperature using (2.1) and (3.9).

Figure 6 shows simulated results for a 50-year period using the stochastic daily temperature input (3.9). Each year represents end of season survivorship results for a single cohort of 1000 individuals. Survivorship in the 50 year simulation ranges between 0.75% and 4% with a median of 2.3%. For many insect species, such as grasshoppers, shifts in end of season survivorship of only 1% or 2% may be sufficient to signal an outbreak year (a year when the insect is recognized as a significant pest) or the onset of conditions favorable for an outbreak in a subsequent year. For example, a high percentage of adult survivorship usually leads to high egg production, which may be a precursor for an outbreak in the following year. To make predictions with regard to actual prey density, it is essential to link yearly
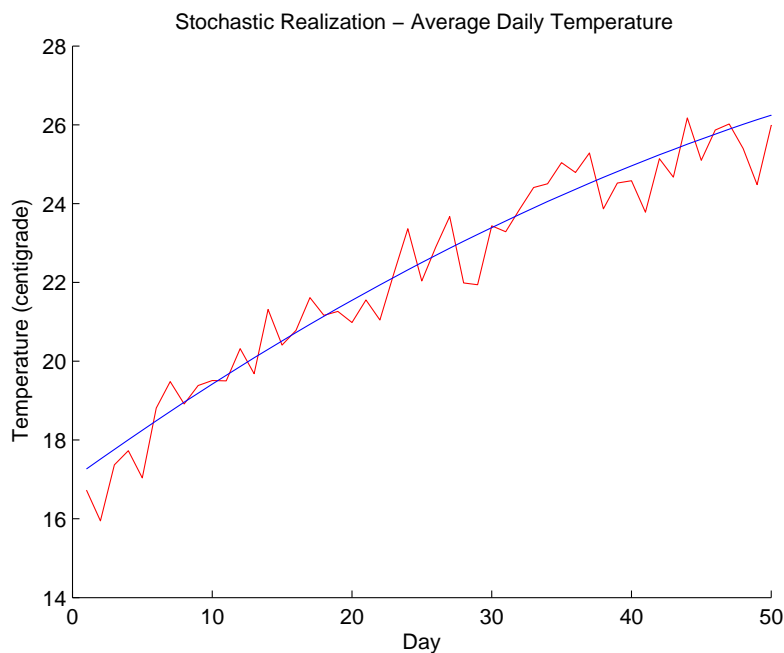
FIGURE 5. Seasonal average daily temperature as a first-order autoregressive process (re: equation (3.9)).

cohort results with year-to-year dynamics. With grasshoppers, that would include linking adult survivorship to egg production and egg hatch rate, both of which are strongly weather related.

4. **Conclusions.** The model presented in this work has several advantages. First, it can be easily modified to investigate additional ecological questions associated with climate change, such as changes in food quality, vegetation density, initial (birth, hatch) mass, size dependent mortality, and predator dynamics. For example, it is predicted that elevated CO_2 levels may increase the amount of vegetation and in turn provide an advantage for cryptic prey. To investigate the effect of increased vegetation and its role on predation, one can let the various attack rates ($\alpha_{i,j}$) differ. On the other hand, increased vegetation is predicted to have lower food quality, thus requiring prey to employ compensatory foraging behavior and increase the number of meals required. For example, grasshoppers have been observed to eat twice as much when food is diluted to half its original nitrogen content (Raubenheimer & Simpson [43]); in grasshoppers this occurred by eating twice as many meals, not by eating larger meals. To examine what effect reduced food quality may have on survivorship and predation, it is only necessary to increase the value of x_{mid} in equation (2.3). Size-dependent mortality can be included in the model by letting the temperature zone attack rates be size dependent, such as in Luttbeg et al. [37] or Logan & Wolesensky [35]. The initial mass of a prey species may depend on climatic conditions, such as winter severity. For simulations used in the model, we assumed that all were of the same initial mass ($m(0) = m_{\mathrm{mid}}(0) = 8$ mg.). In actuality, the initial mass of a species may be better represented by a mass
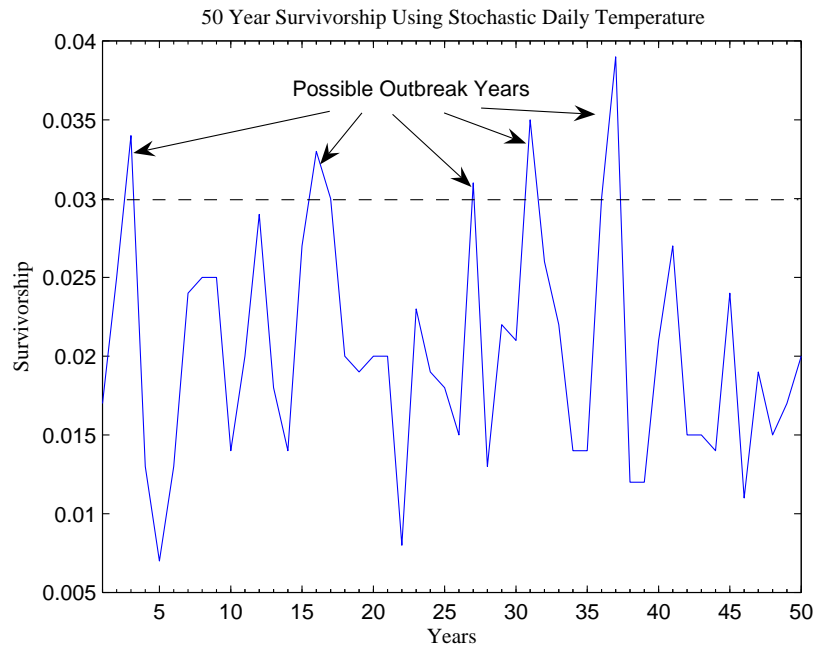
FIGURE 6. End-of-season survivorship for 50 years with a stochastic temperature input.

distribution function. By selecting the initial mass of individuals using a density function, the model can be used to see what effect various initial distributions have on survivorship and adult mass. The predator-prey system we modeled had a constant predator density, but the model can be adapted in a straightforward manner to include predator dynamics. Predator density is used in determining prey survival (equation (2.8)) and prey vigilance (equation (2.7)); using a variable predator density presents no difficulties in either of these equations. Last, and most important, by using the simple structure of temperature-dependent activity zones the model presents a rational mechanism for including temperature into predator-prey dynamics (see also Logan & Wolesensky [35]).

Simulations of the model using parameters that are appropriate to a predator-prey system for wandering spiders and grasshoppers in a high plains environment provide insight into how changes in the daily average temperature effect prey survivorship and predation. Simulations show a significant increase in prey survivorship when the daily average temperature increases in increments of $0.5°$ C (Figures 3 and 4). Interestingly, the increase in survivorship does not come at the expense of predation. To the contrary, simulations predict that predation will increase when the daily average temperature is increased, suggesting that an increase in daily average temperature may benefit both the predator and the prey (if one assumes that increased predation is advantageous to the predator population). Additionally, simulations show that including prey vigilance leads to lower predation, but at the expense of reduced overall survivorship due a greater increase in starvation (Figure 4). This leads to the conjecture that for some arthropod prey, mortality attributed

to the presence of predators is an important factor in controlling prey populations. Further, by comparing the results for both ignorant and non-ignorant prey, model predictions illustrate how decision-making on the individual level can lead to consequences that are not beneficial for the population. By employing vigilance, an individual prey may avoid certain death in the presence of a predator, but the consequence of doing so leads to negative consequences for the entire population.

With the reality of global climatic change, it is increasingly important to include temperature when modeling predator-prey interactions involving ectotherms. This work has two goals: first, to present a rational, mechanistic model for the inclusion of temperature into a terrestrial ecosystem involving exothermic predators and prey, and, second, to verify the usefulness of such a model by making qualitative predictions using parameters that reflect an actual predator-prey system. In addition, we presented results of the model using both ignorant and non-ignorant prey. The main conclusion of these simulations is that temperature changes play a key role in prey survivorship and predation and can simultaneously provide conditions favorable for both predator and prey.

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