INSECT DEVELOPMENT UNDER PREDATION RISK, VARIABLE TEMPERATURE, AND VARIABLE FOOD QUALITY

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Abstract. We model the development of an individual insect, a grasshopper, through its nymphal period as a function of a trade-off between prey vigilance and nutrient intake in a changing environment. Both temperature and food quality may be variable. We scale up to the population level using natural mortality and a predation risk that is mass, vigilance, and temperature dependent. Simulations reveal the sensitivity of both survivorship and development time to risk and nutrient intake, including food quality and temperature variations. The model quantifies the crucial role of temperature in trophic interactions and development, which is an important issue in assessing the effects of global climate change on complex environmental interactions.

1. **Introduction.** A central challenge in population ecology is to understand how key interactions can be integrated into a coherent model of population regulation. It is increasingly appreciated that multiple factors operate simultaneously. Such factors include environmental conditions, food quality, and animal behavior, especially in the presence of competing species or predators, or in foraging strategies (Dunham et al. [13], Grant & Porter [19], Dunham [13], Belovsky & Joern [2], Schmitz et al. [48], Schmitz [47], Pitt [44], Danner & Joern [11]). Because of the difficulty, or even impossibility, in synthesizing many different concepts into a single coherent study, most models of population regulation deal with only one or two critical factors. Yet, incorporating many such interactions involving individual-based attributes into population models may be key to their resolution.

Temperature is a key driving force affecting ectotherm physiology, and it has many important ecological consequences (Logan[1] et al. [34], Grant & Porter [19], Dunham [13], Stamp & Casey [49], Gilbert & Ragworth [16], Gillooly et al. [18]). Feeding, metabolism, and development rates are strongly temperature dependent. Temperature variation can also affect the interactions of prey with predators. Both

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[1]Citations to Jesse A. Logan and to the author, J. David Logan, both occur in this article.

predator and prey activity must be coincident; many arthropods have activity periods bounded by upper and lower threshold temperatures, and temperature changes can shift the interaction periods (Joern et al. [25], Logan et al. [39], Logan & Wolesensky [40],[41]). Slower development rates can also mean additional time spent in those stages where predation risk is greater. Global climate change, which may lead to increased or decreased average temperatures, or larger stochastic variations in temperature, can have a strong effect on underlying critical interactions, and it is important to examine these effects in the context of consumer responses (Joern et al. [25]).

For insect herbivores such as grasshoppers, the availability of food bulk is seldom an issue; but existence of sufficient food with quality above a minimum level is. The natural decrease of protein availability over a growing season causes the C:N ratio in food to increase, thereby decreasing food quality. An insect grazer must therefore increase its intake rate to meet its nutritional demands. However, lower temperatures may make this adjustment impossible, leading to increased mortality (Ayers [1], Pitt [44]). Furthermore, if the prey is aware of predators, then prey vigilance may force the prey into refuge or inactivity, reducing its foraging effort, and again its nutrient needs cannot be met (Houston et al. [22], Lima [30], Brown et al. [7], Danner & Joern [11]).

Many papers have examined the behavioral trade-off between nutrient acquisition and predation risk (e.g., see Lima [30]). Simply stated, feeding options with higher nutrient gain often carry higher risk. As a result, there are many studies regarding behaviorial characteristics that satisfy nutrient requirements while avoiding predation (Gilliam & Fraser [17], Lima & Dill [31]). These studies pose issues such as: how a forager uses time allocation or habitat selection to lessen predation risk (Brown [6]); trade-offs between feeding rates and safety within a patch (Lima & Dill [31], J. S. Brown [5]); how prey optimally select a vigilance level to maximize fitness (Houston et al. [22], Houston & McNamara [23], McNamara & Houston [42]); and, how time-dependent risk drives anti-predator behavior and risk allocation (Lima & Bednekoff [32]). Recent discrete models that include foraging and risk based on probability are presented in Luttbeg et al. [33] and Wolesensky & Logan [52].

In this communication we present a simple model of insect population dynamics that includes temperature and resource variability and prey vigilance in the presence of predators. The goal is to model, in continuous time, the mass development of an animal through its juvenile period as a function of predation risk, environmental temperature, and nutrient intake. The individual mass dynamics scales up to the population level through food-limited mortality and a predation rate that depends upon size and temperature. Under constant parameter assumptions the model is analytically tractable; for time-dependent parameters, numerical simulations show the sensitivity of abundance and development times to risk, nutrient intake, and temperature variations. The major difference between this study and others is the explicit inclusion of temperature dependence as a driving force for consumer phenology and mortality. The model is *metered* in that average daily quantities, such as search time and average body temperature, are computed on a shorter (hourly) time scale. Our focus is on a terrestrial arthropod interaction, e.g., a grasshopper-spider system in grassland environments, but the results may apply to other trophic interactions as well. The outputs, or predictions, are development time and survivorship. Taken separately, model results can be analyzed easily
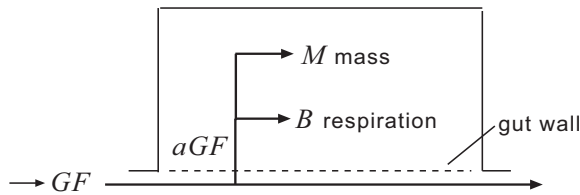
FIGURE 1. Compartmental model of an insect consumer. Food of density F and flow rate G enters at rate FG; a fraction a is assimilated across the gut wall and into the organism's system, where some is used for growth (structure) and the remaining for maintenance (respiration).

TABLE 1. Quantities and Dimensions

Quantity	Name and dimensions
F	Food density (mass per volume)
G	Grazing rate (volume per time)
a	Conversion efficiency (dimensionless)
M	Biomass growth (mass)
B	Respiration rate (mass per time)
θ_b	Average daily body temperature (degrees C)
v	vigilance (dimensionless, $0 \leq v \leq 1$)

with regard to changes in a given mechanism. Treated together, however, it is not clear a priori how all three mechanisms interact to affect model predictions. Our intention is to examine this issue for a cohort of insects. For example, what does it take to maintain the same development period? Under higher temperatures that are environmentally favorable, can the insect increase its vigilance and thus increase its survivorship? What is the best behavioral strategy if environmental temperatures decrease? Similarly, if the species is to maintain survivorship, how should its behavior change in the face of temperature increase or food quality decrease? How all these factors come together to affect population dynamics and development rates is the subject of this work.

2. **The model.**

2.1. **Individual mass dynamics.** The model for the individual is based on a dynamic energy budget (Gurney & Nisbet [20]). Figure 1 shows the compartments and associated rates. Food of density F is consumed at rate G. It enters the digestive tract and a fraction a is assimilated across the gut wall into the animal's system by a complex of metabolic pathways. The assimilated nutrients then are divided between biomass growth (structure M) and respiration (maintenance B). The biomass is the *currency*, and it may be the carbon biomass, the total carbon and nitrogen biomass, or the mass of some essential nutrient. The quantities and their dimensions are shown in the accompanying table. The model depends upon the average daily body temperature θ_b of the prey, and its vigilance level v. We are not considering stoichiometric conditions that might constrain different nutrient concentrations to maintain homeostasis (for example, see Logan et al. [37],[38]).

We do not assume separate autotroph (plant) dynamics. Rather, we assume that food is abundant, but food density, which is related to nutritional quality, may be a function of time, $F = F(t)$. This is true for insects like grasshoppers where the quantity of food is high, but food quality, measured in terms of the carbon-to-nitrogen ratio, is a limiting factor. For example, the C:N ratio increases over a summer growing season as nitrogen availability decreases in plants. Vigilance, a dimensionless constant between zero and one, is a parameter that measures the animal's behavioral response to the presence of predators. High vigilance means reduced foraging effort and decreased predation risk, while low vigilance implies increased foraging with higher predation risk. The vigilance may be a function of predator numbers, or it may be a behaviorial parameter set by the animal as an evolutionary stable strategy to maximize its fitness (J. S. Brown [6], Houston & McNamara [23]), or with the aim of minimizing the ratio of predation risk to nutrient intake (Gilliam's rule); for example, see Houston et al. [22]. One way to interpret vigilance is to relate $1 - v$ to the time spent foraging, or the foraging effort. Yet another view is that vigilance depends on the animal's recent feeding history, or satiation. A hungry animal may always forage under hunger conditions, regardless of the risk.

An individual's dynamics is expressed by the balance law

Growth rate = Assimilation rate − Respiration rate.

In symbols,

$$\frac{dM}{dt} = aGF - B.$$

In this model we are considering nymphs, or juveniles, and we therefore do not include energy devoted to reproduction; nor do we include storage. We impose the following assumptions:

1. The conversion efficiency depends on body temperature $a = a(\theta_b)$, with

$$\frac{da}{d\theta_b} \geq 0.$$

2. The grazing rate depends on a power of the biomass and otherwise depends on temperature, vigilance, and food quality: $G = g(\theta_b, v, F)M^\alpha$, $\alpha > 0$. We expect

$$\frac{\partial g}{\partial \theta_b} \geq 0, \ \frac{\partial g}{\partial v} \leq 0, \ \frac{\partial g}{\partial F} \leq 0.$$

Here, g is the volume that an organism takes in per unit time, per unit size of the organism.

3. The respiration rate B depends linearly on total biomass and otherwise depends upon temperature and food quality: $B = b(\theta_b, F)M^\beta$, $\beta > 0$. We expect

$$\frac{\partial b}{\partial \theta_b} \geq 0, \ \frac{\partial b}{\partial F} \geq 0.$$

In summary, we can therefore write the biomass growth rate equation as

$$\frac{dM}{dt} = a(\theta_b)g(\theta_b, v, F)FM^\alpha - b(\theta_b, F)M^\beta. \tag{2.1}$$

Our assumptions that G and B depend upon a power of mass M must be refined. Generally, through allometric relationships, the mass is proportional to L^3, where L is a characteristic length of the organism. The values $\alpha = \frac{2}{3}$ and $\beta = 1$ imply that assimilation is proportional to the animal's cross-sectional area, while the metabolic

rate depends upon its volume. This assumption implies that the size of an organism will approach a limiting value, which is the classic Bertanaffly law. On the other hand, if $\alpha = \beta = 1$, then both the assimilation rate and metabolic rate depend on volume, and the organism will increase in size exponentially over some time period. In the terminology of Gurney & Nisbet ([20], p 96), these two models are the *cross-sectional* model and *volume* model, respectively. One can argue for other power laws, for example $\beta = \frac{3}{4}$ (J. H. Brown et al. [4]). In the sequel, we develop the dynamics in the context of the volume model.

How a, g, and b depend upon body temperature, food density, and vigilance depend upon further constitutive assumptions. We assume that the grazing rate is given by

$$g(\theta_b, v, F) = r(\theta_b)(1 - v)\left(\frac{g_m F_m}{F}\right),\qquad (2.2)$$

where F_m is the maximum available food density, and g_m is the grazing rate at the maximum. The grazing rate g is maximum when there is no risk ($v = 0$), and it is zero at maximum risk ($v = 1$). The linearity in v is the same assumption made by Houston et al. [22]. In this model, if the food quality decreases by a factor of 2, then the grazing rate doubles. Body temperature-dependence, defined by the function $r(\theta_b)$, is discussed below with respect to all the rates. The conversion efficiency a, or fraction of the ingesta that crosses the gut wall and is assimilated, is temperature-dependent because, at higher temperatures, the substrate-enzyme reactions and absorption rates increase. The conversion rate may also depend upon food density because food density can determine residence time in the gut; however, we do not include this assumption in this model. We represent

$$a(\theta_b) = a_0 r(\theta_b),\qquad (2.3)$$

where a_0 is a constant, $0 < a_0 < 1$. Finally, we assume the respiration rate varies with both body temperature and food density, and we assume

$$b(\theta_b, F) = r(\theta_b)(b_0 - b_1 F).\qquad (2.4)$$

Our assumption of a linearly decreasing function of food density means that respiration will increase as the food density becomes less. In this case, increased grazing and foraging efforts to maintain nutrient intake cause an increased energy expenditure that offsets the decrease energy required to digest the lower quality food. For other organisms, for example, *Daphnia*, there is evidence that the metabolic rate increases with food density (K. Rinke & J. Vijverberg [46]).

In summary, the *master equation* for individual mass dynamics is

$$\frac{dM}{dt} = r(\theta_b)\left(a_0(1 - v)\, g_m F_M - (b_0 - b_1 F)\right) M.\qquad (2.5)$$

In this model, where food abundance is assumed, the net intake is constant and the insect compensates for lower food density by increasing grazing. We expect that the body temperature and food density depend upon time as environmental conditions change, i.e., $\theta_b = \theta_b(t)$, $F = F(t)$. The boundary conditions are

$$M(0) = M_0, \quad M(T) = M_f,$$

where M_0 is the initial mass and M_f is the final mass at full development; both quantities are specified. The horizon time T, which is the length of the nymphal period, is determined as the stopping time when M_f is reached. The model may be modified to include a range, or interval, of target masses.

In Section 4 we indicate how to determine the set of parameters for a generic grasshopper.

2.2. **Temperature-dependent development.** Generally, the development rate of a terrestrial, poikilothermic arthropod with respect to body temperature is strongly nonlinear. The body temperature depends upon the temperature of the microhabitat and the animal's ability to thermoregulate (Casey [8], Chappell & Whitman [10], Lactin et al. [28]). For example, grasshoppers thermoregulate by body orientation with respect to the sun. The microhabitat temperature depends upon the structure of the habitat, the ambient air temperature, and the solar power index, which is a measure of the sunlight falling on the environment. In this section we discuss these issues and motivate a choice for the temperature dependence $r(\theta_b)$ in the master equation (2.5).

In many life-history studies, the cumulative development ξ, measured in degree-days (normalized, $0 \leq \xi \leq 1$), is chosen as the quantity that gauges progress through the nymphal period. The development rate $r = R(\theta_b)$, in degree-days/day is a function of body temperature and has been measured for many organisms. Generally, the development rate is a strongly nonlinear function of temperature as illustrated in the generic plot is shown in figure 2. Over time, the body temperature varies with $\theta_b = \theta_b(t)$; thus the development stage at time t is

$$\xi = \xi(t) = \int_0^t R(\theta_b(s))ds,$$

and full development (maturity) occurs at the time T for which $\xi(T) = 1$. The temperature history, either deterministic or stochastic, is an input to the system. Other studies of temperature-dependent insect phenology include Bentz et al. [3], Logan & Bentz [35], Jenkins et al. [24], Logan & Powell [36], Gilbert et al. [15], and Logan et al. [39]. Digestion modulation in grasshoppers in variable temperature environments has been studied by Wolesensky et al. [51].

Other physiological variables involving size can also serve as development measures. In the present model we use biomass M as the development progress variable, and we apply allometric relationships to connect development in degree-days to mass. Dyer's rule and Przibram's law (Wigglesworth [50]) both imply that body size increases geometrically as a function of development. Therefore, we assume the general relationship

$$M = M_0 \left(\frac{M_f}{M_0} \right)^{\xi}, \quad 0 \leq \xi \leq 1,$$

where M is the mass, M_0 is the initial mass at birth or hatching corresponding to $\xi = 0$, and M_f is the mass at maturity when $\xi = 1$. It follows that the rate of mass development in terms of degree-day development is

$$\frac{dM}{dt} = \ln \left(\frac{M_f}{M_0} \right) MR(\theta_b(t)).$$

Comparison to the master equation (2.5) shows that the temperature dependence of mass development has the same nonlinear form as the development rate in degree-days as shown in figure 2. Temperature dependence of digestion processes are often modeled by a Q_n rule, which requires that the rate doubles for every n degrees (C) increase in temperature. If θ_0 is a reference body temperature, then the rate would contain a factor $2^{(\theta-\theta_0)/n}$, or equivalently, $e^{(\theta-\theta_0)/\Delta}$. Here, $\theta = \theta_b$. But the Q_n rule
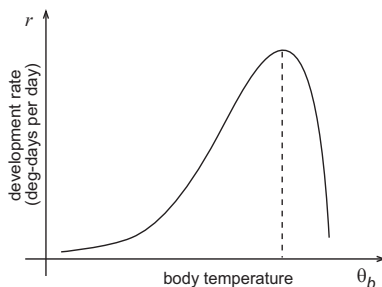
FIGURE 2. The general shape of the nonlinear development rate for many terrestrial arthropods. A functional form is given by equation (6).

only holds in a narrow range of temperatures near the reference temperature, and this factor does not reflect the general nonlinearity shown in figure 2. A global form that holds over a wide range of temperatures has been obtained from fitting experimental data. Here we use the Lactin et al. [28] form

$$R(\theta) = e^{\alpha\theta} - e^{\alpha\theta_0}e^{(\theta-\theta_0)/\Delta} - \lambda,$$

which was developed for various species of grasshoppers. As one can observe, this form is similar to the Q_n rule. In the master equation (2.5) we normalize this rate by dividing by the maximum value $R_{\max}$, so that it takes the value 1 at the optimal body temperature. Thus,

$$r(\theta) = \frac{1}{R_{\max}} \left(e^{\alpha\theta} - e^{\alpha\theta_0}e^{(\theta-\theta_0)/\Delta} - \lambda \right), \quad \theta = \theta_b. \tag{2.6}$$

Consequently, in our model, the grazing rate, the metabolic rate, and the assimilation rate all contain this same temperature factor. The parameters α, λ, Δ, and θ_0 are chosen to fit rates for various species, many of which are given in Lactin et al. [28].

We may include instar development as follows. Let f be the number of juvenile instars. In each instar $(j = 1, 2, ..., f)$ there is a target, cumulative mass M_j that the animal must reach to graduate to the next instar. The completion of the jth instar is therefore the time t_j for which $M(t_j) = M_j$. Thus $T = t_f$ is the nymphal period. We remark that the model can be refined to include an interval of masses suitable to reach full development, rather than a single value. This generalization would allow for development at different sizes, which is observed (Logan et al. [36]).

The model (2.5)–(2.6) provides a comprehensive tool for the simulation of growth in an environment with dependence on temperature, food density, and the prey's level of vigilance. Often the most difficult task is to determine the key parameters. In Section 4 we show how values of $a_0, g_m, F_M, b_0, b_1, M_0$, and M_f are obtained.

Prior to presenting the results of simulations, and before including population dynamics, we indicate how development time T depends upon food density, vigilance, and average body temperature in the case that all the parameters are time-independent, and θ_b, F, and v are constant values. In this special case we may solve (2.5) to obtain
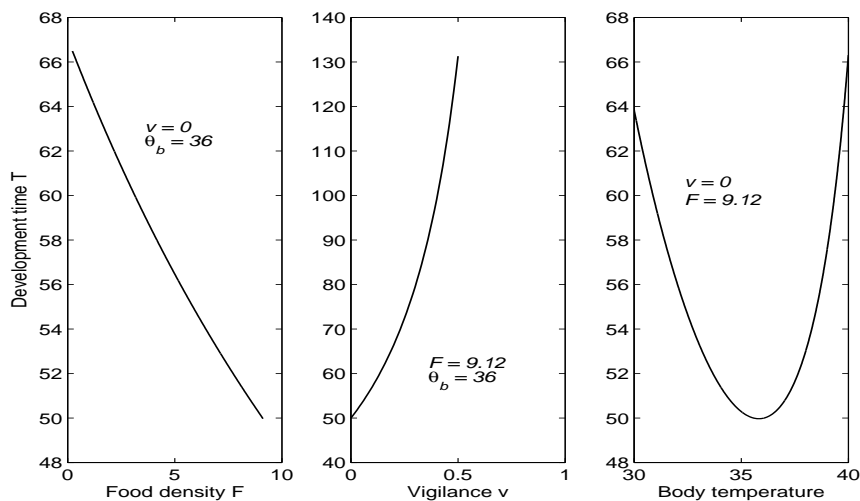
$$M = M_0 e^{r(\theta_b)[ag_m F_M(1-v)-b_0+b_1 F]t},$$

FIGURE 3. Plots showing how the nymphal period T depends upon each of the three parameters, F, v, and θ_b, with the remaining two held fixed. The value $F = 9.12$ corresponds to maximum available food density, and $\theta_b = 36$ corresponds to the body temperature that maximizes the development rate. No vigilance means maximum foraging effort.

which represents exponential growth. Therefore the nymphal period, or time for development, is

$$T = \frac{1}{r(\theta_b)[ag_m F_M(1-v) - b_0 + b_1 F]} \ln\left(\frac{M_f}{M_0}\right).$$

Using parameters calculated in Section 4, we have

$$T = T(\theta_b, F, v) = \frac{1}{r(\theta_b)} \frac{\ln 25}{0.048 - 0.0798v + 0.0018F}.$$

Figure 3 shows how T varies over ranges of the three indicated variables. As expected, development time decreases with increased food density and increases with increased vigilance, and there is an optimum body temperature that minimizes the development period.

3. Mass-dependent population dynamics.

3.1. **A population model.** The next goal is to scale up from the individual to the population, i.e., to a cohort of nymphs. We assume that prey mortality consists of two effects, a natural hazard rate $\mu_n = \mu_n(M, \theta_b)$ representing random events and depending upon size (mass) and body temperature, and a predation rate $\mu_p = \mu_p(\theta_a, v, M, P)$ dependent upon the ambient temperature θ_a, the prey's level of vigilance, its size (mass), and the predator density P. The population dynamics for a prey cohort of population $N = N(t)$ is

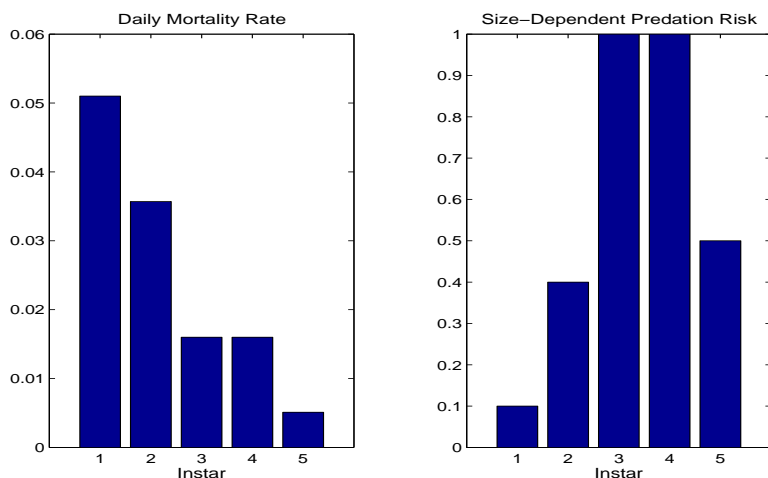$$\frac{1}{N}\frac{dN}{dt} = -(\mu_n + \mu_p), \quad N(0) = N_0.$$

FIGURE 4. Bar graphs of instar-dependent natural mortality rate and predation risk for species of grasshoppers in a grassland environment.

Grasshoppers, for example, have a stage-dependent natural mortality rate (Joern & Gaines [27], Oedekoven & Joern [43]). The mortality rate can also depend explicitly on time, a generalization we do not consider here. In this model we assume the temperature enters the natural mortality rate through the temperature-dependent mass M. Therefore, we assume that $\mu_n = \mu_n(M)$, which is a specified function determined by survivorship experiments. We take

$$\mu_n(M) = m_j, \quad M_{j-1} < M \le M_j, \tag{3.7}$$

where $j = 1, 2, ..., f$ is the instar. Here, m_j is the daily per capita mortality rate, which in the simulations is taken to be constant in each instar (survivorship data shows that, in fact, mortality is higher the first few days of an instar). Figure 4 shows a typical survivorship bar graph for a grasshopper (compare, for example, Joern & Gaines, [27], p431; Oedekoven & Joern [43]). We note that survivorships vary widely, depending on laboratory or field environments.

The functional form of the predator's functional response can be taken as Holling type II or III (see the discrete model by Logan et al. [40]). In the present model we use a mass-action functional response (a type I response) of the form

$$\mu_p = k\delta A P \phi(M), \tag{3.8}$$

where P is the predator density, A is the search rate in area per day per predator, δ is the encounter rate, and k is the fraction of prey captured of those encountered. The factor $\phi(M)$ is a size-dependent predation risk factor. The functional form of $\phi(M)$ depends upon the risk at various sizes. For example, a factor of the form $\frac{\eta\rho}{\eta+M}$, where ρ is the predation rate for newborns and where η is the prey size for which the predation rate is half maximum, the risk decreases as the organism grows. (See the analysis of size-dependent energy budgets in Ledder et al. [29].) On the other hand, if new nymphs have low risk (e.g., predators are uninterested because of small size, or nymphs are protected) and the risk increases up to a maximum size before declining again because of becoming too large for the predator, a functional

form $\rho M^\sigma e^{-\eta M}$ is suggested. This form may be appropriate for spider predation of immature grasshoppers. In the present model we assume the predation risk is dependent upon the developmental stage, or

$$\phi(M) = \phi_j, \quad M_{j-1} < M \le M_j, \tag{3.9}$$

where $j = 1, 2, ..., f$. The ϕ_j measure the daily per capita predation risk in each instar (figure 4).

The encounter rate, a dimensionless quantity, is assumed to have the form

$$\delta(v) = de^{-cv}, \tag{3.10}$$

a decreasing function of vigilance. The factor d is the encounter rate when there is no vigilance, and c is a measure of the prey's effectiveness in detecting and responding to predators. Although these factors appear in the predator's response functional, they can also be interpreted as either prey or predator characteristics. In addition, the encounter rate may be a function of the structure of the microhabitat, e.g., either dense forage or open grassland. Other relations are possible depending upon the behavior and prescience of the prey, fierceness of the predator, and the searching characteristics of the predator (Brown [6]). Satiation is also not included in the simulations; depending upon the prey's recent feeding history, it may relax its vigilance to actively forage. Vigilance itself may depend upon the predator density; a generalized functional relation such as

$$v = \frac{P^n}{P_h^n + P^n}, \quad n \ge 1,$$

or a Heaviside function $v = H(P - P_h)$, both provide a threshold predator density P_h where vigilance is switched on. For the simulations presented in Section 4 we specify a value of v that does not depend upon predator density.

3.2. **Temperature dependence.** Search time may be temperature-dependent, as discussed in Logan et al. [39], [40]. Predation events in insect-arthropod systems depend on both predator and prey being in an active state. Predators may hunt only during certain temperature intervals, and prey may be available only within a range of temperatures. Shifts in the intersection of these two ranges can occur when the temperature varies. For example, body temperature is crucial in insect behavior and development, and there is only a range of temperatures when they are active. In a wolf spider–grasshopper interaction[2] the spider actively hunts only when its body temperature is relatively low compared to grasshoppers, and it avoids the hotter portions of the day (Joern et al. [26]). Figure 5 depicts this shift in a schematic way.

Three temperatures are relevant to describing activity times, namely, body temperature, microhabitat temperature, and ambient air temperature. The microhabitat temperature depends in a complicated manner upon the air temperature, the amount of sunlight falling on the system (the solar power index, measured in watts per meter-squared), and the vegetation structure (grasses or dense vegetation). Body temperature depends on all of these quantities as well, interacting with insect thermoregulation behavior (e.g., body orientation to the sun). To model these complex interactions is beyond the scope of this work. Rather, we take a simpler approach and assume there are upper and lower ambient temperature thresholds θ_{hi} and θ_{lo} between which both predator and prey are active. The joint activity

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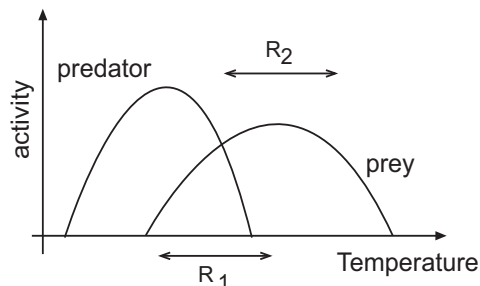[2]This remark refers to crawling wolf spiders (lycosid) that do not build webs.

FIGURE 5. Diagram showing how a shift in the daily temperature range, from R_1 to R_2, can dramatically lessen the possible interaction times between a predator and a prey.

time $\alpha(t)$ on day t is the fraction of the day when the hourly ambient temperature lies between these thresholds. Specifically, if $\theta(\sigma, t)$ is the hourly temperature on day t, where σ is in hours ($0 \leq \sigma \leq 24$), then

$$\alpha(t) = \frac{1}{24} \text{meas}\{\sigma : \theta_{\text{lo}} \leq \theta(\sigma, t) \leq \theta_{\text{hi}}\}.$$

Including this assumption in the model makes the dynamics metered, where a daily quantity is computed from dynamics on a smaller time scale. We chose to work with the ambient temperature rather than the complex microhabitat temperature, which depends on so many other environmental quantities. We then use experimental data gathered by Harrison & Fewell [21] to relate the body temperature θ_b of the prey to the ambient air temperature θ. (Data were taken for *M. bivittatus* at night and on a clear sunny day in a top of the stalk model.) We compute the hourly ambient temperature $\theta(\sigma, t)$ as follows. We assume the average daily temperature throughout a season is generated as a stochastic process $\Theta(t)$ with $\Theta(0) = \theta_0$ fixed. Then we take

$$\theta(\sigma, t) = \Theta(t) + \mathbf{A}(t) \sin \frac{\pi \sigma}{12},$$

where $\mathbf{A}(t)$ is a (stochastic) daily amplitude.

We now address the issue of where the joint activity factor enters into the functional response. For a discrete time model, where search time appears explicitly in the functional response, it is natural to consider the activity time as a factor that either reduces or increases the search time (Logan et al. [39], Logan & Wolesensky [40]). For continuous time models, however, the search time is infinitesimal and is divided out to create, in the limit, a predation rate, as was done in equation (3.8); the search time does not appear on the right side. However, in this case it is equally valid to include the joint activity factor $\alpha(t)$ as a part of the encounter rate d. Clearly, encounters are lessened at lower activity levels and increased at higher levels. Consequently, we modify equation (3.10) by

$$\delta = \delta(v, t) = d_0 \alpha(t) e^{-cv}.$$

For simulations we are motivated by a grasshopper-spider interaction, and we assume that there is only an upper temperature threshold θ_{hi} representing the maximum temperature spiders are active, and no lower threshold. Thus, grasshoppers are always present and susceptible to predation. This is consistent with field data (Joern et al. [26]) showing spiders are particularly active during the morning and

evening hours when cooler temperatures prevail. Then the activity time is computed as

$$\alpha(\theta(t)) = \frac{1}{24}\text{meas}\{\sigma : \Theta(t) + \mathbf{A}(t)\sin\frac{\pi\sigma}{12} \le \theta_{\text{hi}}\}. \tag{3.11}$$

Therefore, the activity time increases on days when the average daily temperature is lower.

To summarize, the final form of the individual mass–population dynamics model is:

$$\frac{dM}{dt} = r(\theta_b)\,(a_0(1-v)\,g_m F_M - (b_0 - b_1 F))\,M, \tag{3.12}$$

$$\frac{dN}{dt} = -\left(\mu_n(M) + kde^{-cv}\alpha(t)AP\phi(M)\right)N, \tag{3.13}$$

$$M(0) = M_0, \quad N(0) = N_0, \tag{3.14}$$

where $\mu_n(M)$ and $\phi(M)$ are given by (3.7) and (3.8), and $\theta_b = \theta_b(t)$, $\theta = \theta(t)$, with $\alpha(t)$ given by (3.11). The mass development rate $r(\theta_b)$ is given by (2.6), and the termination condition is $M(T) = M_f$, which determines the nymphal period T. Clearly, increased vigilance decreases predation risk but decreases foraging effort. Lower temperatures slow development and increase mortality. How all these factors interrelate and how robust the model is to variations are discussed in the next section.

4. **Parameter values and simulations.** A set of benchmark parameters is used to simulate the mass development and population dynamics, (3.12)–(3.13). We assume the weight (mass) of the insect at hatching is $M_0 = 8$ mg, and the weight at full development is $M_f = 200$ mg, both dry weights. The food density and grazing values have to be consistent with development. We compute g_m, F_M, b_0, and b_1 as follows. The mass M at any time is related to the development ξ in degree-days via

$$M = M_0\left(\frac{M_f}{M_0}\right)^\xi, \quad 0 \le \xi \le 1.$$

Therefore the change in M per day in terms of the change in ξ per day is

$$\Delta M = \ln\left(\frac{M_f}{M_0}\right)M\Delta\xi.$$

We assume that, at constant optimum body temperature θ_b^*, the insect's maximum growth rate in degree-days per day is 0.02 degree-days per day. Therefore, the insect will require at least 50 days to mature and the maximum increase in mass per day is

$$\Delta M = \ln\left(\frac{M_f}{M_0}\right)M\Delta\xi = \ln(25)(0.02)M = 0.064M.$$

Optimum growth occurs when there is no vigilance ($v = 0$) and $r(\theta_b^*) = 1$. Therefore, from equation (3.12), at maximum food density F_m, we have

$$(0.7g_m F_M - (b_0 - b_1 F_M)) = 0.064,$$

where we have taken the assimilation rate to be $a_0 = 0.7$ (comparable to measured values). At this maximum growth rate we assume the respiration rate is 20% of the net intake, or

$$b_0 - b_1 F_M = (0.2)(0.7g_m F_M). \tag{4.15}$$

It follows that
$$g_m F_M = 0.114 \text{ day}^{-1}.$$
Then the grazing rate g_m can be computed as follows. The adult 200 mg insect is assumed to have a crop structure that holds 0.5 ml of food. If it eats 5 meals per day when the food quality is maximum, then it consumes a total of 2.5 ml of food per day. This gives
$$g_m = \frac{2.5}{200} = 0.0125 \text{ ml/day} \cdot \text{mg}.$$
This corresponds to a maximum food density of
$$F_M = 9.12 \text{ mg/ml}.$$
This value is a reasonable estimate when compared to the carbon and nitrogen in a leaf; it is measured in mg of dry mass that contributes to the growth of the insect, per ml of plant material.

Finally, we determine the respiration constants b_0 and b_1. From (4.15) we have
$$b_0 - b_1 F_M = 0.016.$$
This assumes a respiration rate that is 20% of the net intake rate. If food density decreases, we expect that the respiration will require greater expenditure of energy caused by increased grazing and foraging. At half the maximum food density, or at 4.56 mg/ml, we assume the respiration rate increases to 30% of the maximum intake, or
$$b_0 - 4.56 b_1 = (0.3)(0.7 g_m F_M) = 0.024. \tag{4.16}$$
Now, (4.15) and (4.16) may be solved simultaneously to obtain
$$b_0 = 0.0324, \quad b_1 = 0.0018.$$

Our assumption regarding respiration differs from the assumption of Rinke & Vijverberg [46], who assume, for *Daphnia*, that maintenance increases with food supply due to the costs of digestion. They observed that the maximal maintenance coefficient was significantly reduced under food shortage, with up to a 50% reduction with no food. Based on terrestrial insects, grazing expenditures exceed digestion costs in our model. This may be a result of insects having to chew the indigestible fiber in the plants they consume.

The predation and vigilance parameters are taken to be
$$k = 0.5, \ A = 100, \ P = 0.01, \ d = 0.5, \ c = 4,$$
and the parameters in the rate function (2.6) are (Lactin et al. [28]):
$$\alpha = 0.119357, \ \Delta = 8.348083, \ \theta_0 = 44.186047, \ \lambda = -0.0748, \ R_{\max} = 0.02.$$
Values for the natural mortality rate and the size-dependent predation factor are given in figure 4.

The body temperature as a function of air temperature is modeled by a piecewise linear function from the experimental data in Harrison & Fewell [21], and it is shown in figure 6. Specifically, below 17°C the body temperature is equal to the air temperature. As the air temperature rises the insect quickly (over the interval $17° \leq \theta \leq 22°$) thermoregulates, and its body temperature increases to 36°, after which it is maintained at a constant level.

One important observation is that the mass and survivorship curves are relatively robust to stochastic variations of temperature; that is, they do not exhibit the strong variations of the average daily temperature—they are smoothed out. On the other
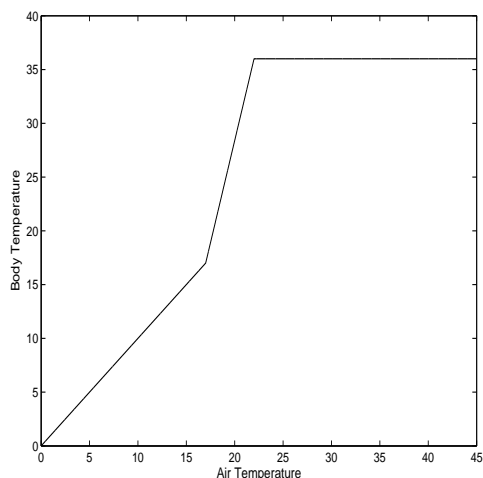
FIGURE 6. The body temperature vs. air temperature for a thermo-regulating grasshopper.
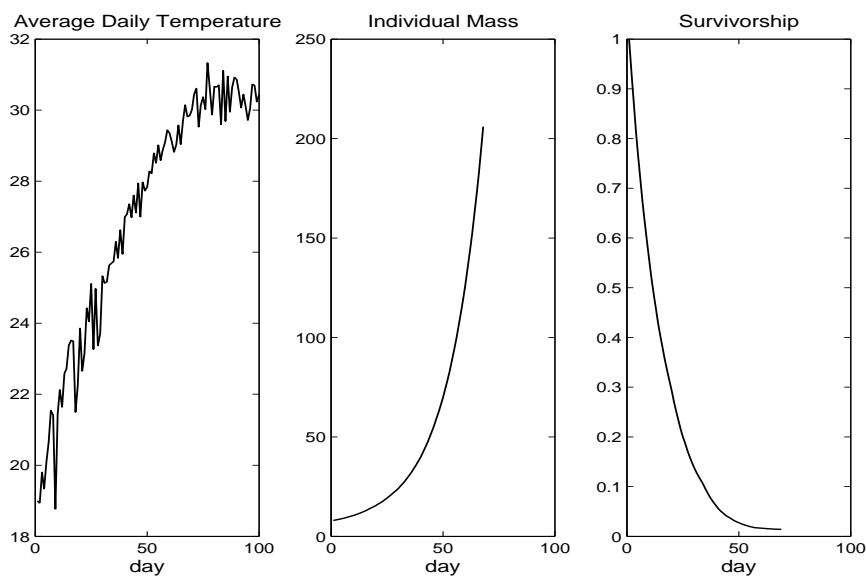

FIGURE 7. Simulation of the model (3.12)–(3.13): the stochastic input of temperature over a 100-day period, the mass of an individual over its nymphal period, and the survivorship of a cohort.

hand, the final output of values T and survivorship at the end of the nymphal period were strongly sensitive to the amplitude of the temperature variation on each day. See the discussion below. Table 2 shows the results of several simulations. Values of the nymphal period T and the percent survivorship (denoted in the sequel by $\%N$) at the end of the period are calculated for different levels of vigilance v and initial temperature $\theta_0 = \Theta(0)$, the temperature on the first day of the season. The

TABLE 2. Development period T and survivorship $\%N$ for various values of vigilance and temperatures.

	$\theta_0 = 17$		$\theta_0 = 19$		$\theta_0 = 21$	
v	T	$\%N$	T	$\%N$	T	$\%N$
0	75	0.4	68	1.5	60	7.4
0.1	84	1.0	75	2.8	68	9.0
0.2	93	1.5	84	3.6	77	9.2
0.3	108	1.5	98	3.7	91	7.5
0.4	–	–	119	2.7	110	4.9

expected daily temperature on day t ($0 \leq t \leq 100$) is $E(\Theta(t)) = \theta_0 + 0.2547t - 0.0014t^2$, which fits temperature data collected during a period beginning June 1 at a western Nebraska site. The daily amplitude is fixed at 10 degrees, and food density is maximum ($F_M = 9.12$). The *dash* in the table means the nymphal period exceeded 120 days, which is considered death for the cohort. Figure 7 shows, graphically, a typical simulation.

The first observation is that the insect has an optimal vigilance level that maximizes its survivorship. For example, at $\theta_0 = 19$ the survivorship is maximized at a value near $v = 0.3$, or 70% foraging effort.

Also observe that the insect can maintain stability in its nymphal development under increased temperature by increasing its vigilance level, thereby decreasing predation risk and increasing considerably its survivorship. For example, at $\theta_0 = 19$ with $v = 0.1$ development period is 75 days. If temperature increases by an average of $2°$, the animal can increase its vigilance to 0.2 with an accompanying decrease in predation to nearly maintain its nymphal period (77 days) while increasing its survivorship by over 200% (from 2.8 to 9.2). On the other hand, if the average temperature is lowered to 17, the insect must lower its vigilance, thereby increasing its risk; its survivorship drops significantly to 0.4.

Table 2 reveals that regulation of a stable survivorship under temperature changes is impossible, regardless of the level of vigilance. Thus, temperature is the overriding factor in survivorship. At low temperatures the development period is long, causing the insect to experience high mass-dependent mortality rates in critical instars. Predation from spiders appears to be only a minor regulatory factor in controlling populations.

The simulations may also be examined to assess responses to food quality. At $\theta_0 = 19$, Table 3 shows the nymphal period and survivorship for various vigilance levels when the daily food density decreases linearly, $F(0) = F_M - (F_M/200)t$. Compare to column 2 of Table 2, which is for constant, maximum food density. The effect of a lower food density is a few additional days to develop, more at higher vigilance levels, and a few tenths of percent decrease in survivorship, again at higher vigilance levels. One of the strongest effects observed in the simulations is the sensitivity of the nymphal period and survivorship to the daily temperature amplitude $\mathbf{A}(t)$. Take $\theta_0 = 19$, $v = 0$, with maximum food density; fixing $\mathbf{A}(t) = 7$ gives $T = 62$ and $\%N = 6.3$, while fixing $\mathbf{A}(t) = 13$ gives $T = 75$ and $\%N = 0.53$. We can compare these values to column 2 in Table 2 where $\mathbf{A}(t) = 10$. Decreasing the daily amplitude by 3 degrees decreases the nymphal period 8.8% and increases survivorship over 300%. Increasing the daily amplitude 3 degrees has an equal, but opposite effect. The conclusion is that the insects will experience much greater

TABLE 3. Effect of variable food density.

v	0	0.1	0.2	0.3
T	71	79	91	110
$\%N$	1.4	2.4	3.2	2.9

fitness under uniform temperatures than under erratic temperature variations. This conclusion may have been expected, but not of the order of magnitude indicated.

5. **Concluding remarks.** We have constructed a model of population response (survivorship) and phenology (development period) that depends upon environmental temperature, food density, and predation risk with prey vigilance. The model allows us to assess the changes when three potentially regulatory factors (biophysical, behavioral, and predatory) are interrelated in a single dynamical process. The model simulations confirm intuitively held views that temperature plays an essential, if not the major, role in the regulation of population. One important prediction that is perhaps unexpected is that daily temperature amplitudes affect the dynamics considerably. Therefore, increased temperature uncertainties, such as those that might be expected under global environmental change, lead to significant changes in survivorship and development.

Another general prediction is that the insect can, under a fixed temperature regime, choose a vigilance level that maximizes its survivorship, which is a measure of its fitness. We can also conclude that an insect can maintain a stable development period under a temperature increase by adjusting its vigilance level, and, as a result, considerably increase its survivorship. Under lower temperature regimes, the insect may be able to stabilize its development period by reducing vigilance, but it always comes with the cost of reduced survivorship. In general, under temperature changes, the insect will not be able to stabilize its survivorship by changing its vigilance, even if food density is high. These conclusions again point to temperature as a major driving force in insect population regulation; moreover, higher temperatures are greatly beneficial to insects.

In this model there is no feedback from fecundity of reproducing adults; the initial cohorts are hatched from eggs in the spring laid by females the previous fall. Year-to-year dynamics is a complicated issue that involves the dynamics of reproducing, adult females and survivability of the eggs over the winter. For grasshoppers, for example, these issues involve food quality at the end of the nymphal season, the number of egg clutches and clutch size, environmental conditions like winter severity, and egg fungi and parasitoids. (see Chapman & Joern [9]). We can however, suggest some general implications from our model. First, greater temperatures and optimal vigilance lead to shorter development periods and higher survivorship. This means the adult stage will have a longer end-of-season for reproduction. Under seasonal environmental conditions and sufficient food quality, more clutches with more eggs per adult female will result, giving the possibility of higher hatch rates in the spring. Overall, a model that includes year-to-year dynamics must have a strong stochastic component for the over-wintering period. These ideas are discussed in another communication.

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