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A model of digestion modulation in grasshoppers

William Wolesensky[a,b,*], Anthony Joern[c], J. David Logan[b]

[a] *Program in Mathematics, College of St. Mary, Omaha, NE 68134, USA*
[b] *Department of Mathematics, University of Nebraska, Lincoln, NE 68588, USA*
[c] *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

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Abstract

A phenomenological model is presented that links digestion and gustatory responsiveness for insect herbivores using chemical reactor models for digestion and feedbacks from nutrient titers in the hemolymph that determine internal delays. Numerical simulations under conditions of variable temperature and food quality gave qualitative and quantitative predictions of intermeal behavior coupled to substrate and nutrient concentrations in digestive structures (crop, midgut, and hemolymph system) that reasonably reflect available results for grasshoppers. Direct links between foraging behavior and the physiological process of digestion shows that digestion modified by temperature is an important rate-limited step in nutrient acquisition because of differential effects on different rates. Key results from the model, many deserving further empirical and theoretical study, include: (1) elevated metabolism at high temperature outstrips increased nutrient gain from increased gut throughput rates, indicating that the nutrient budget is regulated by temperature-dependent hemolymph use. (2) Depending on parameter choices, both absorption- and digestion-limitation is possible, regulated in part by midgut retention time of digesta. (3) For conditions studied here, foraging delay takes precedence over hemolymph feedback and may be explained by the need to balance diets. (4) Unless increased temperatures accompany lower food quality, insect herbivores will be unable to fully compensate for decreased food quality. (5) There is a physiological advantage to foraging at the extreme temperature range of well-studied development curves (>38–40 °C) although even higher temperatures beyond this point could be fatal, indicating the need for risk assessment models of such decisions.

Keywords: Absorption-limited; Digestion; Foraging; Ecophysiology; Grasshoppers; Insects

1. Introduction

Nutrient titers in the hemolymph have been recognized as playing a key role in the gustatory responsiveness of insects (Abisgold and Simpson, 1987; Simpson and Simpson, 1990; Simpson and

* Corresponding author.
E-mail addresses: bwolesen@math.unl.edu (W. Wolesensky), dlogan@math.unl.edu (J.D. Logan).

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Raubenheimer, 1993). Thus, to form an integrated approach to describe intermeal behavior requires linking digestion and hemolymph titers to gustation. The complex digestion process itself is often described in the context of chemical reactor theory (Penry and Jumars, 1986; Dade et al., 1990; Woods and Kingsolver, 1999; Jumars, 2000a,b; Logan et al., 2002, 2003), which provides a compromise between mechanistic detail and phenomenological responses. In this paper we build upon and extend the conventional reactor models of digestion in the works cited above to include a hemolymph system along with feedbacks that control foraging and intermeal delays. The alimentary system we consider consists of a saccular structure (the crop, modeled by a semi-batch reactor) connected in series to a tubular structure (the midgut, modeled by a plug flow reactor (PFR)). Both are connected to a hemolymph system, modeled as a continuously stirred tank reactor (CSTR) (Fig. 1).

This model differs significantly from previous chemical reactors models in both scope and purpose. The goal of much of the previous work in this area has been to examine some type of optimality argument (Penry and Jumars, 1986, 1987; Karasov and Hume, 1997; Jumars, 2000a; Logan et al., 2002, 2003) with respect to the various types of reactors. While one cannot overstate the value of these models, it is important to note that these models exclude the role that temperature plays in digestion. For a complete review of chemical reactor models of digestion the reader is referred to Wolesensky and Logan (in press). The aim of the model we present here is to provide a chemical reactor model that captures (in a phenomenological sense) the digestion and foraging behavior of insects by providing a link between nutrient concentrations in the hemolymph with the gustatory responsiveness of the insect. By including temperature in reaction rates, feedbacks, and digestion flow through speed, we are able to make quantitative predictions of foraging behavior under different temperatures. In a similar manner we are able to make predictions of foraging behavior under different food qualities.

Nutrient acquisition in insects can be categorized generally as follows. After consumption, substrates are broken down into nutrients components which are then transported across the gut boundaries into the hemolymph system. In the hemolymph, nutrients are then distributed to metabolic activities such as somatic maintenance and respiration, growth, reproduction, and storage. Food can be highly variable in both availability and nutritional quality, especially for herbivores, and needs change depending upon physiological and biochemical requirements. We view the hemolymph as providing a constantly updated indicator of an insect's nutritional state, which reflects properties such as the nutritional quality of recent meals and the time since the last meal (Abisgold and Simpson, 1987; Simpson and Simpson, 1990; Chyb and Simpson, 1990; Simpson and Raubenheimer, 1993). It is conjectured that the insect uses this information to directly feedback to its

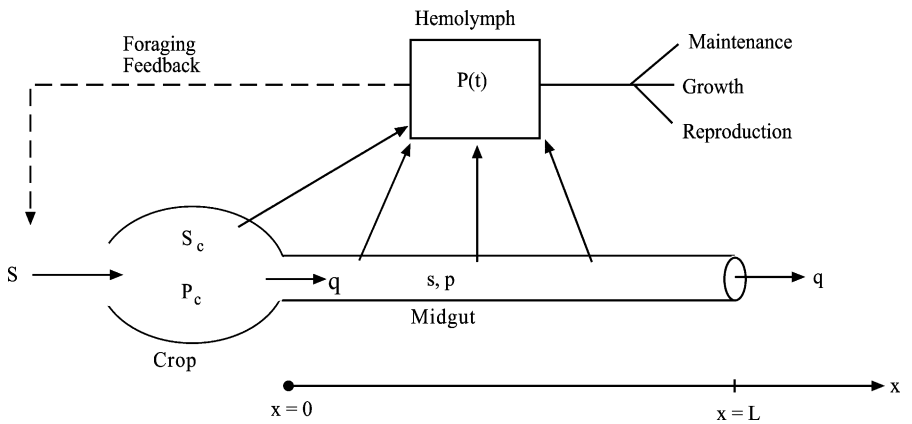

Fig. 1. Schematic of alimentary system with feedbacks. Food is loaded instantaneously into the crop where a small amount of reaction and absorption may occur as the digesta moves into the midgut. It passes through the midgut at a speed dependent on its quality; in the midgut it breaks down and the nutrient products are absorbed along its length into the hemolymph system. There, nutrients of concentration $p(t)$ are distributed to the grasshopper's energy needs; upper and lower concentration threshold levels trigger the cessation and onset of feeding.

own gustatory responsiveness. The overall aim of this paper is to provide an explanatory, mechanistic model that can be used to make predictions of nutrient concentrations in the crop, midgut, and hemolymph, as well as predictions of intermeal delays and total nutrient uptake. We couple nutrient concentration levels in the hemolymph with the assumption that foraging follows an exponential distribution (Gross, 1986) to determine the intermeal interval. Both variable food quality and variable temperature are included in the model. The former is selected through a normal random variable, and the rate constants in the chemical reactions are dependent upon the external, environmental temperature. We greatly simplify the underlying chemical kinetics of substrate breakdown and absorption by assuming a two-step reaction where a substrate **S** breaks down into a nutrient product **P**, which is then absorbed into the hemolymph. Therefore, we are ignoring issues such as control of pH, water and salt levels, targeted ratios of essential nutrients, and other factors that play a role in digestion modulation. It is straightforward to adapt the model to simulate detailed biochemical kinetics. We observe that, in spite of the simplifications, we are still able to develop a model that reasonably simulates insect behavior and that predicts titers of both **S** and **P** in the digestive structures.

Because of the three digestive structures and the large number of variables in the model, we adhere to the notational convention that variables relative to the crop have superscript c, variables relative to the midgut have superscript m, and those relative to the hemolymph have superscript h. These superscripts should not be confused with powers.

2. The crop–midgut–hemolymph model

2.1. Model of the crop

The function of the crop in the model is two-fold. First, the crop regulates the quantity of food ingested during each meal. We assume a fixed volume of food V_0 enters the crop each time a meal is consumed, and then empties at a rate dependent upon the quality of the food (Yang and Joern, 1994) and the external temperature. Secondly, there is substrate reaction and possible nutrient absorption in the crop. As is the case with for many insects, the degree of reaction and absorption is small compared to that occurring in the midgut (Srivastava, 1973; Wigglesworth, 1984).

Saccular organs such as the crop can be modeled as semi-batch reactors (Logan et al., 2002). These are characterized by instantaneous filling and perfect mixing, while emptying at volumetric flow rate $Q_n^{\mathrm{c}} = Q^{\mathrm{c}}(t_n)$ where t_n is the time when the nth meal is ingested. The flow rate Q_n^{c} remains constant until the crop empties, at which time it becomes 0; then at the instant $t = t_{n+1}$ when the $(n+1)$ meal is ingested, the flow rate Q_{n+1}^{c} is once again determined and the cycle repeats. Letting $t_{\mathrm{e}} = V_0/Q_n^{\mathrm{c}}$ be the time to empty, we find that the volume of material in the crop during the time interval (t_n, t_{n+1}) is modeled by

$$V^{\mathrm{c}}(t) = V_0 - Q_n^{\mathrm{c}}(t - t_n), \quad t_n \le t < t_{\mathrm{e}}, \tag{1}$$

$$V^{\mathrm{c}}(t) = 0, \quad t_{\mathrm{e}} \le t < t_{n+1}. \tag{2}$$

The determination of the flow rate Q_n^{c}, which depends upon food quality, is discussed in Section 2.5.

The assumption of instantaneous filling arises from experimental observations showing that the crop fills on the order of minutes, while the process of digestion is on the order of hours. Thus, feeding time is ignored in the model.

We consider a model problem where food containing a substrate **S** is loaded into the crop. While in the crop, **S** reacts with an enzyme **E** to produce a nutrient product **P**; schematically,

$$\mathbf{S} + \mathbf{E} \rightarrow \mathbf{P}.$$

It is straightforward to include more detailed chemistry with several chemical species. A small amount of the product **P** may then be absorbed across the crop wall into the hemolymph system where it is then distributed for use in the organism's dynamic energy budget (Kooijman, 1995; Nisbet et al., 2000). In the midgut the product nutrient is absorbed to a greater degree (Section 2.2). In this paper we do not consider the actual distribution of the nutrient to the energy budget, but only the fact that some energy currency is allocated; our main goal is to model how nutrient concentration levels in the hemolymph can trigger the onset and cessation of feeding.

A model for the kinetics in the crop can be obtained by applying the law of mass balance to the substrate and nutrient in the crop. Mass balance dictates that the

time rate of change of a chemical species in the crop is equal to the rate that the species is flowing out combined with the rate that it is being absorbed while in the crop. Letting $S^c = S^c(t)$ and $P^c = P^c(t)$ represent the molar concentrations of **S** and **P**, and proceeding in the usual manner (Levenspiel, 1972; Gurney and Nisbet, 1998) we obtain the differential equations with the initial conditions:

$$(V^c(t)S^c)' = -V^c(t)r^c(S^c, \theta) - Q_n^c S^c,$$
$$S^c(t_n) = S_n^c,$$
$$(V^c(t)P^c)' = V^c(t)r^c(S^c, \theta) - V^c(t)a^c(P^c, \theta) - Q_n^c P^c,$$
$$P^c(t_n) = 0.$$

In these equations, $t_n < t < t_{n+1}$. The initial conditions are given at the time of the nth feeding. Here $r^c(S^c, \theta)$ denotes the reaction rate for the substrate-enzyme kinetics for **S** and $a^c(P^c, \theta)$ represents the absorption rate for nutrient product **P**. Note that both the reaction and absorption terms depend on the concentration of the various concentrations as well as the external temperature $\theta = \theta(t)$. It is well recognized that temperature plays a vital role in the thermal regulation of digestion in insects (Hoffman, 1984; Karsov, 1988; Chappel and Whitman, 1990), but is routinely ignored in most digestion models. We give precise forms for these rates in Section 2.4. When $V^c(t) \neq 0$ we expand the derivatives on the left sides of the preceding equations and simplify to get the following set of differential equations for the substrate and nutrient product concentrations in the crop:

$$\frac{dS^c}{dt} = -r^c(S^c, \theta), \quad V^c(t) \neq 0 \tag{3}$$

$$S^c(t_n) = S_n^c, \tag{4}$$

$$\frac{dP^c}{dt} = r^c(S^c, \theta) - a^c(P^c, \theta), \quad V^c(t) \neq 0 \tag{5}$$

$$P^c(t_n) = 0, \tag{6}$$

when $V^c(t) = 0$ we simply set both $S^c(t) = 0$ and $P^c(t) = 0$. Observe that in the time intervals when material is in the crop, flow rate from the crop is a constant, thus the flux terms involving Q_n^c cancel.

2.2. Model of the midgut

Digesta, which contains both substrate and nutrient, exits the crop into the midgut. The midgut is modeled as a PFR (Logan et al., 2002) of length L and constant cross-sectional area A (Fig. 1); it is characterized by continuous flow of material in the axial direction. The flow is orderly in so much that material exits the midgut in the same sequence that it entered. We assume that the material is perfectly mixed in the radial direction, and we assume that mixing in the axial direction is negligible. These assumptions ignore the presence of both diffusion and counter currents that may occur in the axial direction in the midgut.

Let $S^m = S^m(x, t)$ and $P^m(x, t)$ denote the concentrations of the substrate **S** and nutrient **P**, respectively, at position x and time t in the midgut, $t_n < t < t_{n+1}$. Proceeding as in Logan et al. (2002) or Woods and Kingsolver (1999), we apply mass balance to a small, arbitrary section of the midgut to obtain the following coupled system of reaction-advection equations with initial and boundary conditions:

$$\frac{\partial S^m}{\partial t} + Q_n^m \frac{\partial S^m}{\partial x} = -r^m(x, t, S^m, \theta), \tag{7}$$

$$S^m(x, 0) = 0, \; S^m(0, t) = S^c(t), \tag{8}$$

$$\frac{\partial P^m}{\partial t} + Q_n^m \frac{\partial P^m}{\partial x} = r^m(x, t, S^m, \theta) - a^m(x, t, P^m, \theta), \tag{9}$$

$$P^m(x, 0) = 0, \; P^m(0, t) = P^c(t). \tag{10}$$

The quantity Q_n^m (length time^{-1}) denotes the constant speed of material though the midgut in the interval $t_n < t < t_{n+1}$, r^m is the reaction rate for substrate breakdown in the midgut, and a^m the absorption rate of the nutrient **P** across the epithelium of the gut wall. The reaction and absorption rates can vary both spatially and temporally and, as well, depend on concentrations and temperature (Logan et al., 2002). The boundary conditions at $x = 0$, the entry to the midgut, are the concentrations of the substrate and nutrient exiting the crop.

2.3. Model of the hemolymph system

We model the hemolymph system as a CSTR of constant volume V^h where the nutrient product enters from both the crop and midgut, and exits to supply

the organism's energy budget (maintenance, growth, reproduction). Using a net production model (Gurney and Nisbet, 1998; Kooijman, 2000; Lika and Nisbet, 2000; Ledder et al., 2004) for the energy budget, we let the constant d be the rate of energy use for maintenance and $V^{\mathrm{h}}a^{\mathrm{h}}(P^{\mathrm{h}},\theta)$ be the rate of energy use for growth and reproduction. We have made the assumption that only the growth and reproduction term of the energy budget is temperature dependent. Here we assume that the maintenance term represents an "average" energy consumption rate independent of temperature, but the model can be easily adjusted to let the maintenance term also be temperature dependent (which it most surely is in poikilotherms). Applying mass balance to the nutrient product **P** of concentration $P^{\mathrm{h}}(t)$ in the hemolymph, we obtain

$$V^{\mathrm{h}}\frac{\mathrm{d}P^{\mathrm{h}}}{\mathrm{d}t} = A\int_0^L a^{\mathrm{m}}(x,t,P^{\mathrm{m}},\theta)\,\mathrm{d}x + V^{\mathrm{c}}(t)a^{\mathrm{c}}(P^{\mathrm{c}},\theta) - (V^{\mathrm{h}}a^{\mathrm{h}}(P^{\mathrm{h}},\theta)+d), \tag{11}$$

$$P^{\mathrm{h}}(0) = P_0^{\mathrm{h}}. \tag{12}$$

Although the volume of the hemolymph can be variable (Bernays, 1990), we assume that it is constant in this model. The first term in Eq. (11), a nonlocal integral term, comes from absorption occurring along the entire length of the midgut, while the second term on the right side is the contribution of the nutrient from the crop. The last term represents the distribution of **P** to the energy budget.

2.4. Reaction and absorption rates

Biochemical reactions for substrate breakdown and membrane transport involve many chemical species and can be exceedingly complex. In this model we substantially simplify the complex chemical dynamics by using the Michaelis–Menten model for the enzyme-substrate reaction as well as for the midgut absorption (membrane transport) process. Thus, we are modeling transport of molecules across the gut membranes by simple diffusion rather than facilitated transport. Temperature plays a central role in the rate that these processes occur. Behavioral thermoregulation in insects, particularly grasshoppers, is well documented (reviewed by Uvarov, 1977; Wigglesworth, 1984; Chappel and Whitman, 1990; Lactin and Johnson, 1998), and the physiological consequences of temperature on metabolic rates, gut throughput speed, and net energy has been the source of more recent research (Harrison and Fewell, 1995; Gilbert and Raworth, 1996). Thus, to simulate grasshopper behavior and adequately model digestion processes it is necessary to build temperature into the various reaction and absorption rates. We incorporate temperature into these rates using $Q_{10} = 2$ (i.e., rates double for every 10 °C-temperature increase; Hoffman, 1984; Karsov, 1988). Although Q_{10} may vary among different processes (Harrison and Fewell, 1995; Gilbert and Raworth, 1996), for simplicity we assume it to be equal to 2 for all processes. We model the daily temperature cycle by the periodic function $\theta = \theta_0 + \alpha\cos(\omega t)$ where $\omega = \pi/12$ and α is the amplitude variation around the value θ_0. Therefore, for substrate breakdown in the crop and midgut we take

$$r^{\mathrm{c}}(S^{\mathrm{c}},\theta) = \frac{W^{\mathrm{c}}S^{\mathrm{c}}}{K^{\mathrm{c}}+S^{\mathrm{c}}}2^{(\theta-\theta_0)/10}, \tag{13}$$

$$r^{\mathrm{m}}(S^{\mathrm{m}},\theta) = \frac{W^{\mathrm{m}}S^{\mathrm{m}}}{K^{\mathrm{m}}+S^{\mathrm{m}}}2^{(\theta-\theta_0)/10}, \tag{14}$$

where W_{c} and W_{m} are the maximum values and K_{c} and K_{m} are the half-saturation values. We assume that the enzyme concentration in the crop is much less than in the midgut and thus have $W^{\mathrm{c}} \ll W^{\mathrm{m}}$. For the absorption rate in the midgut we use Michaelis–Menten kinetics, and we use linear kinetics for the both $a^{\mathrm{c}}(P^{\mathrm{c}},\theta)$ (crop absorption) and $a^{\mathrm{h}}(P^{\mathrm{h}},\theta)$ (energy budget term in the hemolymph). That is,

$$a^{\mathrm{c}}(P^{\mathrm{c}},\theta) = \lambda^{\mathrm{c}}P^{\mathrm{c}}2^{(\theta-\theta_0)/10}, \tag{15}$$

$$a^{\mathrm{m}}(P^{\mathrm{m}},\theta) = \frac{\lambda^{\mathrm{m}}P}{\rho^{\mathrm{m}}+P}2^{(\theta-\theta_0)/10}, \tag{16}$$

$$a^{\mathrm{h}}(P^{\mathrm{h}},\theta) = \lambda^{\mathrm{h}}P^{\mathrm{h}}2^{(\theta-\theta_0)/10}. \tag{17}$$

These kinetics laws are the components of a simplified model. A more detailed model can include realistic kinetics, insofar as such kinetics are known.

In summary, we have developed a mechanistic model of the digestion process that includes a crop structure, a tubular midgut, and a hemolymph system. To reiterate, the model is described qualitatively as follows. Digesta is loaded instantaneously into the crop where a small amount of substrate breakdown and absorption occur; from there it moves into and through

the midgut where most of the reaction and absorption occur. The product nutrients are then assimilated across the gut wall into a hemolymph system where they can be used to satisfy the nutritional needs of the organism. The full mathematical model is a system of differential equations, along with initial and boundary conditions for the unknown concentrations of the substrate and nutrient in the crop, midgut, and hemolymph. However, this model of the digestion process is only the physiological part of the overall problem. The basic question that we are addressing is how digestion might affect intermeal behavior, foraging, and consumption, and vice-versa. We build a framework for these interactions by imposing feedbacks that govern the feeding process.

3. Feedbacks and flow through rates

We now extend the crop–midgut–hemolymph model of digestion to connect nutrient levels in the hemolymph with gustatory responsiveness. Experimental investigations have demonstrated that levels in the hemolymph of both amino acids and sugars provide nutrient-specific influences on feeding behavior in several species of acridids and caterpillars (Abisgold and Simpson, 1987; Simpson et al., 1990; Simpson and Simpson, 1990; Simpson and Raubenheimer, 1993). Using empirical evidence, Simpson and Raubenheimer (1993) concluded that hemolymph parameters, such as nutrient titers, are linked with the gustatory responsiveness of the insect. In particular, they noted that; (1) insects with low concentrations of particular nutrients in the hemolymph (nutrient deficient) were more likely to locomote and forage for food than those insects that are nutritionally replete, and (2) high concentrations in the hemolymph of certain nutrients will inhibit further feeding on food containing that nutrient. We integrate these observations into the model by defining upper and lower thresholds of the nutrient concentration in the hemolymph to either increase or decrease the gustatory responsiveness of the animal. We use an upper threshold value U_{h} (point A on Fig. 2) of the nutrient concentration P^{h} to trigger a response to cease ingestion at the inlet to the crop. As the concentration $P^{\mathrm{h}}(t)$ peaks, and then decreases, we allow for a lower threshold value U_{l} (point B on Fig. 2) where feeding responsiveness is triggered. Fig. 2 illustrates a generic form of P^{h} and the threshold values. Note that the hemolymph feedback just described has the effect of delaying the onset of the next meal if a high quality food has been ingested. This is consistent with behavior described in the literature (Yang and Joern, 1994; Simpson and Raubenheimer, 2000). During the period where nutrient levels are satisfactory, in between the threshold values, we assume that quiescent or foraging behavior may be occurring. Foraging behavior is simulated by selecting a foraging time, which is an exponentially distributed random variable R_{e}; i.e., $\Pr(R_{\mathrm{e}} \leq t) = 1 - \exp(-\eta t)$ (e.g., see Gross, 1986), where η^{-1} is the average foraging time. For our simulations we use $\eta^{-1} = 1.5\,\mathrm{h}$, which is chosen to correspond with the simulated behavior generated in Simpson and Raubenheimer (2000). Once feeding is initiated we assume that the quality of food ingested S_n^{c} is a random variable chosen from a normal distribution with mean μ and standard deviation σ. For the simulation described in this paper, we use data that corresponds to $\mu = 3\%$ (approximately 3 mg/ml) and $\sigma = 1\%$. Of course, the model can also be set to simulate laboratory conditions where there may be no foraging delay or variability in food quality.

Much of the research involving chemical reactor models of digestion has been directed at determining

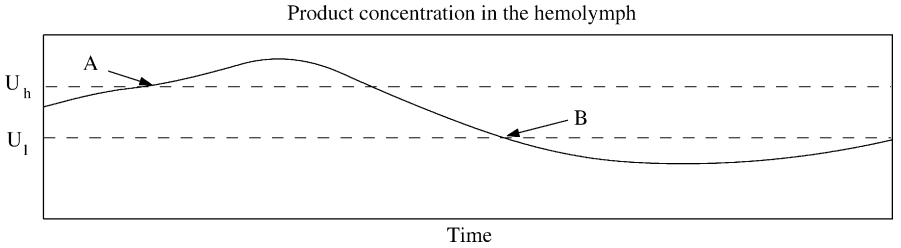

Fig. 2. Point A represents the value in the hemolymph where nutrient levels have exceeded the upper threshold and the insect is satiated. Point B represents the concentration in the hemolymph when nutrient levels have decreased past the lower threshold and gustatory responsiveness is triggered.

the optimal flow through speed with regard to some specific objective criterion, e.g., maximizing absorption rates or digestibility (Penry and Jumars, 1986, 1987; Dade et al., 1990; Jumars, 2000a,b; Logan et al., 2002, 2003). In this work, we are setting a framework for a descriptive, phenomenological model of observed behavior; thus our goal is not to determine an optimality criterion, but rather to define an descriptive model for the rate Q_n^{m} that digesta travels through the midgut. It has been observed empirically that the speed that material travels through the alimentary system is highly dependent upon the nutritional quality of the food ingested (Yang and Joern, 1994). Our model allows for nutritional quality to be sensed using chemoreceptors located on the feet and mouthparts (Blaney and Simmonds, 1990; Simpson and Raubenheimer, 1993). This permits the insect to identify the nutritional quality of the nth meal at the instant of time $t = t_n$ when it is ingested, which immediately modifies the midgut flow through rate Q_n^{m}. We assume that the midgut flow rate remains fixed throughout the time interval (t_n, t_{n+1}), and is again updated at the instant the $(n+1)$st meal is placed in the crop.

It was determined by Yang and Joern (1994) that food residence time for the grasshopper *Melanoplus differentialis* was greatly influenced by diet quality, developmental stage, and temperature. Using nitrogen concentration as a measure of food quality they found that food residence time increased linearly with food quality ($P < 0.001$), thus flow through speed decreases with respect to increasing food quality. We fit the data from Yang and Joern (1994) to obtain the equation

$$Q_n^{\mathrm{m}} = F(S_n^{\mathrm{c}}, \theta) = [(-4.5L)S_n^{\mathrm{c}} + 0.445L]2^{(\theta-\theta_0)/10} \tag{18}$$

which determines midgut speed when the nth meal is consumed (L represents the length of the midgut). For simplicity we assume $Q_{10} = 2$ (the data show a 24% decrease in residence time for a 5 °C increase in ambient temperature). While this formula has the advantage of fitting empirical data (Yang and Joern, 1994), it fails to offer any insight into what physiological processes an insect actually uses to determine flow through speed. It may be that midgut speed not only reflects the quality of the current meal, but also the quality of previous meals remaining in the midgut at the time the current meal is consumed. For example, if a high quality meal remains in the midgut at the time when a low quality meal is ingested, one would expect that this earlier meal may have an effect on the flow through speed. That is, midgut speed may be a weighted average dependent on the meals that remain in the midgut at the time the nth meal is consumed. This idea can be expressed mathematically as

$$\begin{aligned} Q_n^{\mathrm{m}} = [&w_{n-1}F(S_n^{\mathrm{c}}, \theta) + w_{n-1}F(S_{n-1}^{\mathrm{c}}, \theta) \\ &+ w_{n-2}F(S_{n-2}^{\mathrm{c}}, \theta) + \cdots + w_{n-k}F(S_{n-k}^{\mathrm{c}}, \theta)]. \end{aligned} \tag{19}$$

Here $w_{n-i} = w_{n-i}(t_n - t_{n-i})$ represents a weight dependent on the midgut residence time, $t_n - t_{n-i}$, of the $(n-i)$th meal that remains in the midgut at the time t_n when the current meal is consumed, and $S_{n-1}^{\mathrm{c}}, S_{n-2}^{\mathrm{c}}, \ldots, S_{n-k}^{\mathrm{c}}$ represent the initial concentrations of the meals that remain in the midgut at the time the current meal in consumed. The validity of the postulated equation, the values of the weights, and the functional form of the function F represent questions that need further investigation. While it is also likely that the flow through speed depends on the position of digesta in the midgut, we ignore this possibility in this work.

Finally, we note that once the midgut speed Q_n^{m} is determined, we have also determined the crop exiting speed Q_n^{c}. To convert Q_n^{m} into its volumetric equivalent we multiply by the cross-sectional area A of the tubular midgut, i.e. $Q_n^{\mathrm{c}} = AQ_n^{\mathrm{m}}$. In the sequel we replace Q_n^{m} by Q_n and Q_n^{c} by AQ_n in the equations for the midgut and crop.

4. The scaled model

To reduce the number of constants in the model we scale the dependent and independent variables by appropriate reference quantities and thus produce an equivalent, much simpler, dimensionless model. The most difficult scale to determine is the time scale because of the large number of choices. Possibilities include times for the various reaction and absorption processes to occur, the time for the crop to empty, and the time based on midgut speed. Because the model relies heavily on nutrient titers in the hemolymph for feedbacks, and because these titers are strongly affected by digestion occurring in the midgut, we

use the average midgut flow through time (L/Q_{ave}) as the time scale, where Q_{ave} (length time^{-1}) is the average midgut flow through speed (corresponding to $S_n^{\text{c}} = 0.03$). To scale the concentrations we use $S_{\max}$ (mol vol.$^{-1}$), the maximum concentration of the substrate available in the foods supplied to the insect. In summary, the scaled, dimensionless variables are

$$v^{\text{c}} = \frac{V^{\text{c}}}{V_0}, \quad s^{\text{c}} = \frac{S^{\text{c}}}{S_{\max}}, \quad p^{\text{c}} = \frac{P^{\text{c}}}{S_{\max}}, \quad q_n^{\text{c}} = \frac{Q_n^{\text{c}}}{(AQ_{\text{ave}})},$$
$$s^{\text{m}} = \frac{S^{\text{m}}}{S_{\max}}, \quad p^{\text{m}} = \frac{P^{\text{m}}}{S_{\max}}, \quad q_n = \frac{Q_n}{Q_{\text{ave}}}, \quad y = \frac{x}{L},$$
$$p^{\text{h}} = \frac{P^{\text{h}}}{S_{\max}}, \quad \tau = \frac{t}{(L/Q_{\text{ave}})}, \quad T = \frac{\theta}{\theta_0}.$$

With the exception of the scaled temperature T, all dimensionless variables are represented by lower-case letters. Introducing the dimensionless parameters

$$\alpha_1^{\text{c}} = \frac{AL}{V_0}, \quad \tau_n = \frac{Q_{\text{ave}} t_n}{L}, \quad \tau_{\text{e}} = \frac{Q_{\text{ave}} V_0}{LAQ_n},$$
$$\alpha_3^{\text{c}} = \frac{LW^{\text{c}}}{Q_{\text{ave}} S_{\max}}, \quad \alpha_4^{\text{c}} = \frac{\lambda^{\text{c}} L}{Q_{\text{ave}}}, \ \beta^{\text{c}} = \frac{K^{\text{c}}}{S_{\max}},$$

replacing Q_n^{c} by AQ_n, and using the rate expressions defined in (13) and (15), the crop Eqs. (1)–(6) become

$$v^{\text{c}}(\tau) = 1 - \alpha_1^{\text{c}} q_n(\tau - \tau_n), \ \tau_n \le \tau < \tau_{\text{e}}, \tag{20}$$

$$v^{\text{c}}(\tau) = 0, \ \tau_{\text{e}} \le \tau < \tau_{n+1}, \tag{21}$$

$$\frac{\mathrm{d}s^{\text{c}}}{\mathrm{d}\tau} = -\frac{\alpha_3^{\text{c}} s^{\text{c}}}{\beta^{\text{c}} + s^{\text{c}}} 2^{\theta_0/10\,(T-1)}, \tag{22}$$

$$s^{\text{c}}(\tau_n) = s_n^{\text{c}}, \tag{23}$$

$$\frac{\mathrm{d}p^{\text{c}}}{\mathrm{d}\tau} = \left[\frac{\alpha_3^{\text{c}} s^{\text{c}}}{\beta^{\text{c}} + s^{\text{c}}} - \alpha_4^{\text{c}} p^{\text{c}}\right] 2^{\theta_0/10\,(T-1)}, \tag{24}$$

$$p^{\text{c}}(\tau_n) = 0. \tag{25}$$

Next, defining the dimensionless coefficients

$$\alpha_1^{\text{m}} = \frac{LW^{\text{m}}}{Q_{\text{ave}} S_{\max}}, \quad \alpha_2^{\text{m}} = \frac{\lambda^{\text{m}} L}{Q_{\text{ave}} S_{\max}},$$
$$\beta_1^{\text{m}} = \frac{K^{\text{m}}}{S_{\max}}, \quad \beta_2^{\text{m}} = \frac{\rho^{\text{m}}}{S_{\max}}$$

and the rates given by (14) and (16), the midgut Eqs. (7)–(10) become

$$\frac{\partial s^{\text{m}}}{\partial \tau} + q_n \frac{\partial s^{\text{m}}}{\partial y} = -\frac{\alpha_1^{\text{m}} s^{\text{m}}}{\beta_1^{\text{m}} + s^{\text{m}}} 2^{\theta_0/10\,(T-1)}, \ y > 0, \ \tau > 0, \tag{26}$$

$$s^{\text{m}}(y, 0) = 0, \ s^{\text{m}}(0, \tau) = s^{\text{c}}(\tau), \tag{27}$$

$$\frac{\partial p^{\text{m}}}{\partial \tau} + q_n \frac{\partial p^{\text{m}}}{\partial y} = \left[\frac{\alpha_1^{\text{m}} s^{\text{m}}}{\beta_1^{\text{m}} + s^{\text{m}}} - \frac{\alpha_2^{\text{m}} p^{\text{m}}}{\beta_2^{\text{m}} + p^{\text{m}}}\right] \times 2^{\theta_0/10\,(T-1)}, \ y > 0, \ \tau > 0, \tag{28}$$

$$p^{\text{m}}(y, 0) = 0, \quad p^{\text{m}}(0, \tau) = p^{\text{c}}(\tau). \tag{29}$$

For the hemolymph Eqs. (11) and (12) we define the dimensionless parameters

$$\alpha_1^{\text{h}} = \frac{A\lambda^{\text{m}} L^2}{S_{\max} V^{\text{h}} Q_{\text{ave}}}, \quad \alpha_2^{\text{h}} = \frac{V_0 \lambda^{\text{c}} L}{Q_{\text{ave}} V^{\text{h}}},$$
$$\alpha_3^{\text{h}} = \frac{\lambda^{\text{h}} L}{Q_{\text{ave}}}, \quad \alpha_4^{\text{h}} = \frac{Ld}{S_{\max} Q_{\text{ave}} V^{\text{h}}},$$

and the rate given by (17), to obtain

$$\frac{\mathrm{d}p^{\text{h}}}{\mathrm{d}\tau} = \left(\alpha_1^{\text{h}} \int_0^1 \frac{p^{\text{m}}(y, \tau)}{\beta_2^{\text{m}} + p^{\text{m}}(y, \tau)} \,\mathrm{d}y + \alpha_2^{\text{h}} v^{\text{c}} p^{\text{c}} - \alpha_3^{\text{h}} p^{\text{h}}\right) \times 2^{\theta_0/10\,(T-1)} - \alpha_4^{\text{h}}, \tag{30}$$

$$p^{\text{h}}(0) = p_0^{\text{h}}. \tag{31}$$

Finally we nondimensionalize the various feedback quantities. The threshold values in the hemolymph that trigger feeding become $u_{\text{h}} = U_{\text{h}}/S_{\max}$ and $u_{\text{l}} = U_{\text{l}}/S_{\max}$, while the foraging delay is now $\Pr(R_{\text{e}} \le \tau) = 1 - \exp(-\kappa\tau)$, with dimensionless coefficient $\kappa = (\eta L/Q_{\text{ave}})$; the scaled average food quality is given by $\mu/S_{\max}$. The scaled form for the throughput speed is

$$q_n = \left(\frac{1}{Q_{\text{ave}}}\right)[(-4.5L)s^{\text{c}} S_{\max} + 0.445L]2^{\theta_0/10\,(T-1)}. \tag{32}$$

Eqs. (20)–(32), together with the scaled feedbacks, define the complete dimensionless version of the model.

5. Simulation and discussion

Numerical simulations can be obtained using the Runge–Kutta method for the ordinary differential equations, an explicit finite difference scheme for the reaction-advection partial differential equations, and the trapezoidal method for the nonlocal integral term

in the hemolymph equation. A code was written using Matlab version 5.3 (The Math Works Inc., Natick, MA, USA). At 900 MHz the code takes approximately 20 min to execute 21,600 time step (simulates approximately 72 h). The following parameter values were used for the numerical computations:

$A = 0.25\pi$ mm^2	$\theta_0 = 30^\circ$	$\alpha = 10^\circ$
$W^{\mathrm{m}} = 50$ mg/ml/h	$W^{\mathrm{c}} = 0.5$ mg/ml/h	$K^{\mathrm{m}} = 15$ mg/ml
$\lambda^{\mathrm{c}} = 0$	$\lambda^{\mathrm{h}} = 1.04\,\mathrm{h}^{-1}$	$K^{\mathrm{c}} = 15$ mg/ml
$V_0 = 0.125$ ml	$U_{\mathrm{h}} = 0.1$ mg/ml	$U_{\mathrm{l}} = 0.76$ mg/ml
$L = 15$ mm	$S_{\max} = 5$ mg/ml	$V^{\mathrm{h}} = 0.375$ ml
$\lambda^{\mathrm{m}} = 0.195$ mg/ml/h	$d = 0.001$ mg/h	$Q_{\mathrm{ave}} = 4.32$ mm/h

The parameter values W^{m} and K^{m} reflect those found in Woods and Kingsolver (1999) for asocasein ($W^{\mathrm{m}} = 500$ mg/h/ml, $K^{\mathrm{m}} = 1.5$ mg/ml), λ^{m} is the representative of the absorption of proline across the midgut wall of *M. sexta* (Woods and Chamberlin, 1999), while U_{h} and U_{l} are chosen to correspond to the concentration of 7.4 mM proline in the hemolymph (Woods and Chamberlin, 1999). The dimensions of the crop and midgut are a result of measurements taken upon dissection, and Q_{ave} is chosen from the data given in Yang and Joern (1994).

We discuss in detail a sample simulation (of the scaled model), which represents a single realization of a stochastic process, in detail. While more simulations would let us draw better quantitative conclusions, the scope of the work presented here is to show the capabilities of the model and exactly what types of predictions can be obtained. Fig. 3 shows results for the crop and hemolymph from this single simulation representing approximately 72 h of clock time; Fig. 4 shows an exploded view of the middle third of the simulation, and Fig. 5 shows profiles of substrate/product concentrations as foodstuff passes through the midgut. The main features of the simulation include:

1. Simpson and Raubenheimer (2000) showed that grasshoppers were twice as likely to feed during periods of light as compared to periods of dark. In comparing Fig. 3a to Fig. 3b, we see that the model predicts approximately three times the number of meals to be ingested between the time of 06:00 and 18:00 as compared to between 18:00 and 06:00. This prediction is similar to the result attained by Simpson and Raubenheimer (2000), is a result of temperature differences. We use the model to make quantitative prediction between foraging and temperature in the next section.
2. The peaks labeled A and B in Fig. 3c occur during lower temperature cycles. These predicted elevation of nutrient concentrations result from meal timing. Note that Peak A in Fig. 3c followed meals that occurred at low temperatures. To examine the role of temperature in nutrient uptake, we input meals of identical quality into the model, the only difference is that one meal was ingested at 12:00 h (high temperature) while the other was ingested at 24:00 h (low temperature). The results were interesting. Total uptake from the meal varied little (decreased by 1% at lower temperature), even though retention time differed significantly (50% longer for the meal at low temperature). Enhanced metabolism at high temperatures is responsible for this difference, but the model predicts that the insect quickly utilizes the nutrients gained. In constructing the model, we included temperature dependence into the growth and development term of the energy budget (see Eq. (30)). In the time that it took for a single meal ingested at high temperature to pass through the digestive track (the model predicts approximately 1.75 h), there was a *net loss* of nutrient in the hemolymph (nutrient usage from the hemolymph was 14% more then nutrient uptake into the hemolymph) thus explaining the need for insects to forage heavily during periods of high temperature. The meal ingested at low temperature showed a *net gain* of 6% during the same time interval (1.75 h), thus the extended duration of the peaks A and B in Fig. 3c for nutrient titers in the hemolymph are clearly a result of the rate at which nutrients are utilized from the hemolymph.
3. Fig. 3d shows that the amount of uptake of the nutrient P into the hemolymph is much greater during the time periods between 06:00 and 18:00. This can been seen in comparing the relatively flat regions denoted by 1–3, in Fig. 3d, to the other regions. Since temperature was built into only the growth and development term of the energy budget, and the model makes predictions of increased nutrient usage during periods of high temperatures, this translates into the prediction that the insect will exhibit greater growth during the time of day when the temperature is elevated. This hypothesis requires more investigation into energy budgets and how nutrients are allocated for various needs.

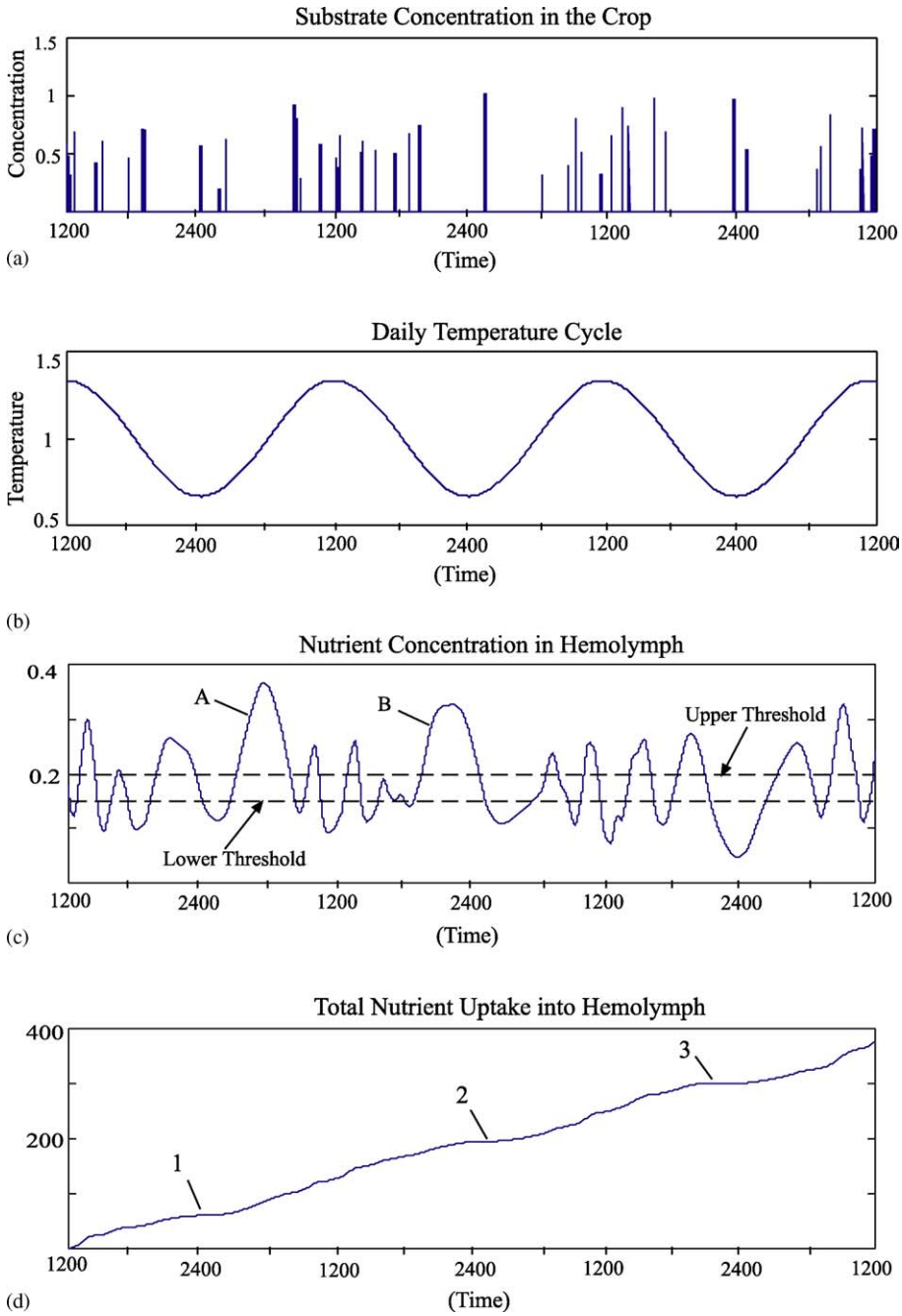

Fig. 3. (a) Shows the concentration of the ingested food, and it also indicates times when the meals occur. (b) Represents the daily temperature cycle used in the simulation. (c) Illustrates the product titers in the hemolymph and (d) is the scaled total product uptake into the hemolymph. The quantities in all figures, with the exception of time, represent scaled quantities.

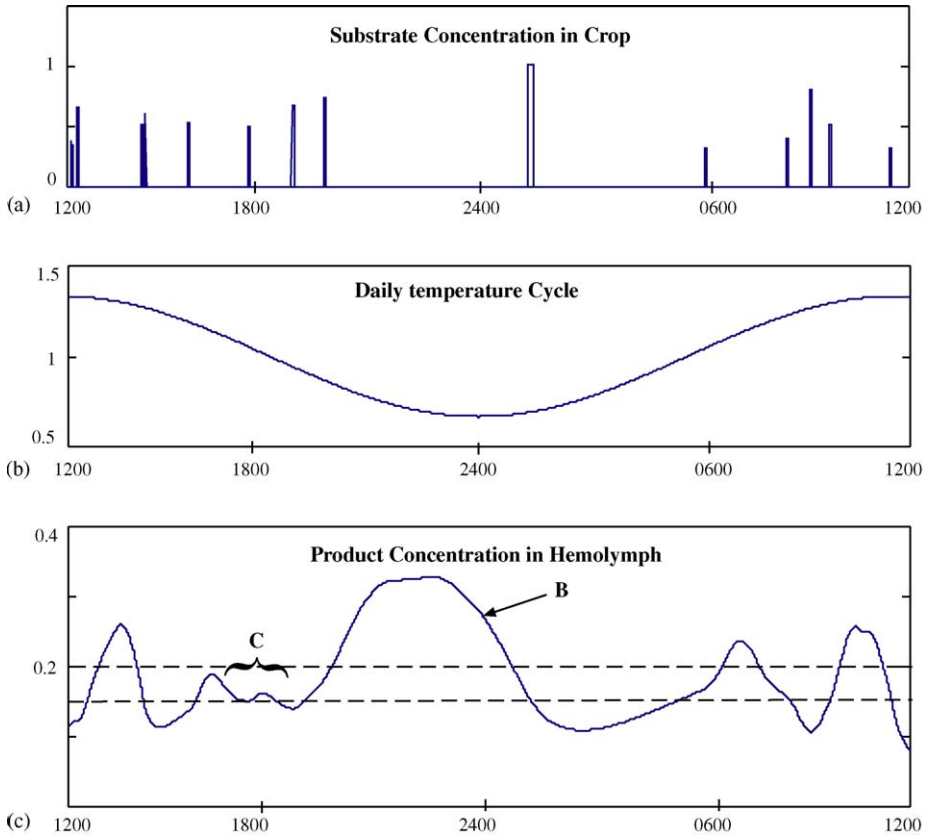

Fig. 4. Exploded view of the middle third of Fig. 3 showing a 1-day simulation. The accumulation and utilization of nutrients from the hemolymph clearly demonstrates the crucial role that the temperature cycle plays in the various reaction and absorption rates.

4. The top row in Fig. 5 shows time snapshots of the concentration of the substrate as it passes through the midgut, while the bottom row shows corresponding time snapshots of product concentrations. For the parameter values used in the simulation, the model is exhibiting absorption-limited behavior rather then digestion-limited behavior (Woods and Kingsolver, 1999; Logan et al., 2003) (the process of reaction and absorption is termed *absorption-limited* if the absorption rate of the nutrient product is slow relative to the reaction rate; this is clearly the case when comparing the two rows in Fig. 5). The model is easily adjusted for different parameter values that lead to a reversal of the roles (i.e. slow reaction, but fast absorption). Increasing retention time in the midgut would tend to allow for more nutrient product to be absorbed across the gut wall into the hemolymph, thus helping to offset the effect of absorption limitation.
5. The investigation of the interplay between digestion and foraging is the motivation for much of the research presented here. We modeled this interdependence in two ways: using nutrient levels in the hemolymph and choosing the foraging time as a random variable from an exponential distribution. To actually determine the length of the intermeal interval we choose the longest time associated with these two criteria. Therefore, in the model the insect will not feed until both criteria have been met, and thus an insect may not necessarily eat even though the upper threshold U_h has yet to be exceeded. The model exhibits this behavior where the graph of P^h is decreasing—shown in Fig. 4c at the interval labeled C. When this occurs it is simply a

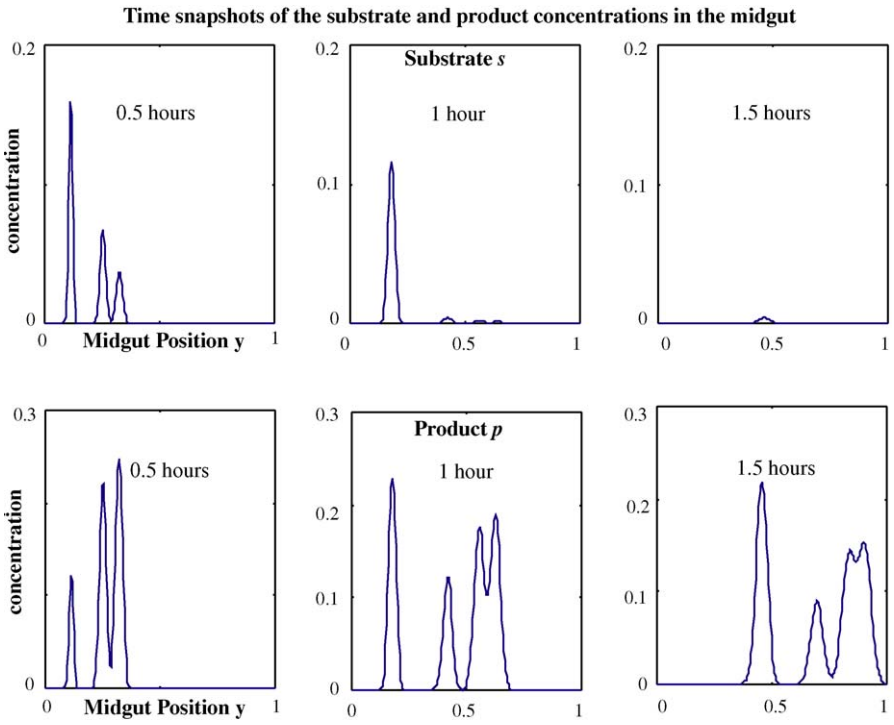

Fig. 5. Plots showing time snapshots of the substrate and product concentrations at various locations in the midgut. Note the rapid reaction of substrate as it passes through the midgut (top row), while at the same time nutrient product is produced and absorbed at a slower rate in the midgut. This is typical of absorption limited gut behavior.

result of the foraging delay taking precedence over the hemolymph feedback. This behavior may be explained physiologically by the need for an insect to balance many complimentary nutrients (Simpson and Raubenheimer, 1995, 1996) and to meet a variety of nutritional needs.

While the five points above discuss features of the current simulation, the model itself has intrinsic value. Being a mechanistic mathematical model, it is extremely flexible. For example, we can determine easily the model's response to constant food quality or a constant temperature regime. In the current simulation we ignore absorption from the crop ($\lambda^c = 0$), but we could readily change the value of this parameter to include nutrient absorption in the crop. Further, we can change the kinetics in the model to be more realistic. In the current model we have used nutrient titers in the hemolymph to help determine gustatory responsiveness. While there is ample evidence (Abisgold and Simpson, 1987; Simpson et al., 1990; Simpson and Simpson, 1990; Simpson and Raubenheimer, 1993) that nutrient titers definitely play a role in gustatory responsiveness, we acknowledge that there are many other factors that play significant roles in determining the onset of a meal (pH levels, predation threats, nutritional stoichiometry, etc.). Adapting the model to include other gustatory factors is straight forward.

Another significant feature of the model is that it allows for a priori estimates of various parameters by repeated simulations. For example, working under the assumption that nutrient titers are driving gustatory responsiveness, we could estimate the parameters in the hemolymph by making repeated simulations for various parameter values and comparing the resulting feeding pattern to those that are empirically observed. The parameter values that lead to a feasible feeding pattern could then be used to determine a confidence interval for the true parameter value.

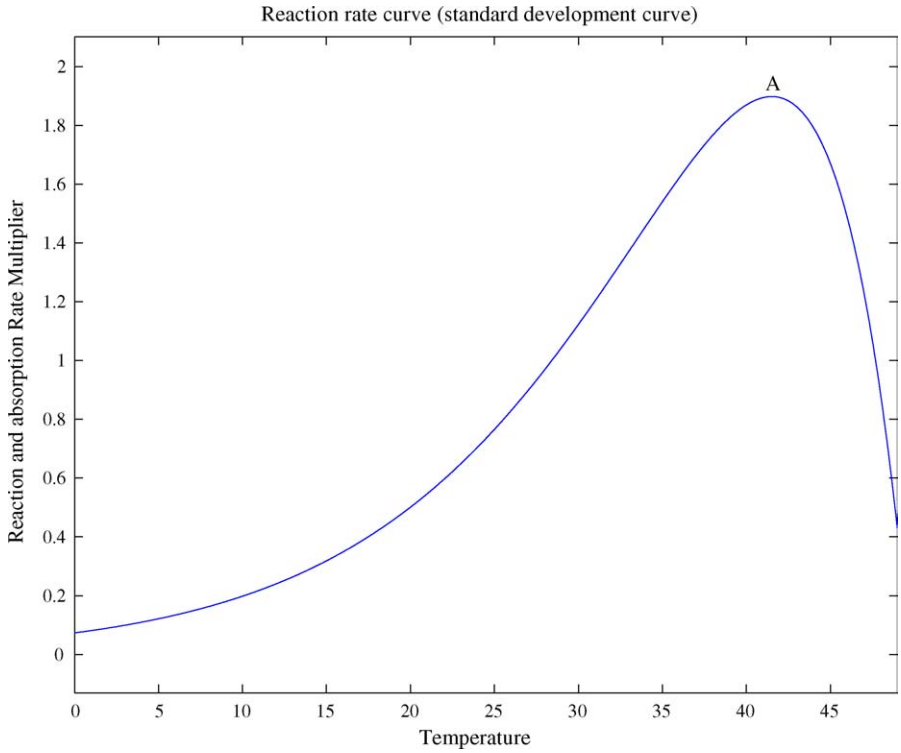

Fig. 6. Standard development curve.

5.1. Deterministic results: foraging

Another ecological issue is understanding the role that temperature and food quality have on foraging behavior. Using the deterministic shell of our model (removing stochasticity from the food quality and the intermeal interval) we can investigate the role temperature and food quality play in determining intermeal behavior and nutrient acquisition into the hemolymph. Replacing the simple "rule of 10" temperature dependence used in the reaction and absorption rates in the model by a standard development curve (Lactin and Johnson, 1998) (Fig. 6), we can make predictions regarding foraging behavior and nutrient uptake.

Fig. 7 shows the response of the model to various food quality and temperature inputs. Fig. 7a shows the predicted effect of food quality on the interaction between temperature and number of meals consumed. The predicted compensatory response to low quality food agrees with empirical data showing that grasshoppers adjust for low quality food by increasing food consumption, which they accomplish through more frequent meals (Simpson and Simpson, 1990). The model also suggest that insects are unable to fully compensate for lower food quality. Fig. 7b shows that the predicted uptake of nutrients into the hemolymph is significantly less for lower quality food, although the number of meals consumed is considerably greater. This suggests that, at a given temperature, insects will be unable to fully compensate for low quality food (e.g., draw a vertical line in Fig. 7b at a given temperature and compare the points of intersection with the curves). But if lower food quality is accompanied by an increase in the average temperature then the model predicts that, in some temperature ranges, the compensatory mechanisms of increased eating and enhanced physiology will be sufficient to meet nutritional requirements (e.g., draw a horizontal line at a given uptake amount in Fig. 7b and compare the intersection points). Additionally, the shapes of Fig. 7a and b follow the same trend as the development curve. This is expected and further validates the accuracy of the numerical solution.

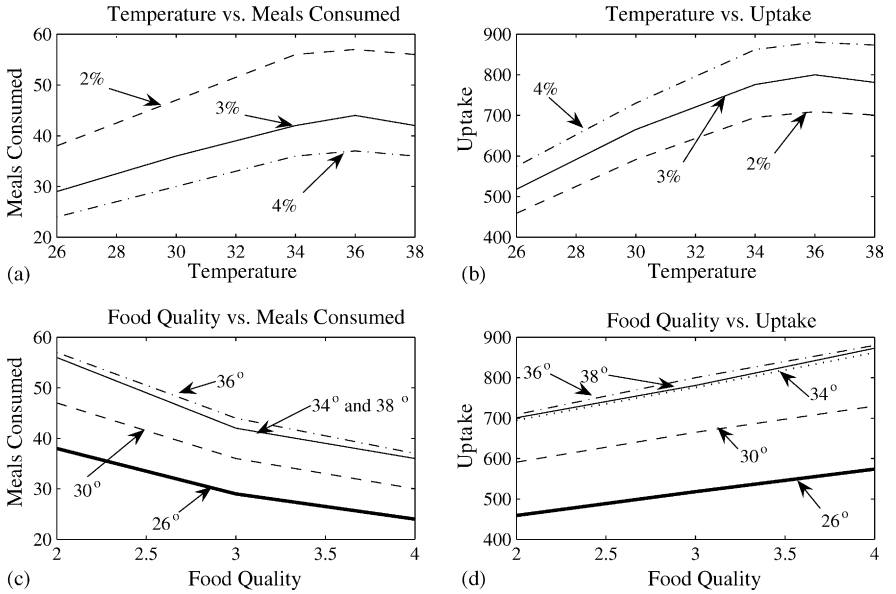

Fig. 7. (a and b) Shows the expected effect of temperature on meal consumption and nutrient uptake. (c and d) Shows the response of the model to varying food quality. As stochasticity has been removed from the model the results shown are actually independent of time. The model falls into periodic behavior after approximately 60 h of simulated time.

Fig. 7c and d give further insight into the interaction between temperature, food quality, nutrient uptake, and the number of meals consumed. Fig. 7c clearly predicts that the number of meals consumed is decreasing with respect to food quality, while Fig. 7d predicts that nutrient uptake will increase with higher quality food. That is, the model makes the prediction that unless increased temperatures accompany lower food quality, grasshoppers will be unable to fully compensate for the decreased food quality. This predicted lower nutrient uptake (Fig. 7d) could have significant population effects by decreasing fecundity and/or increasing the duration of nymphal stages. Increasing the length of various instars may have adverse population effects by expanding the time that grasshoppers are susceptible to predation and disease. Also of interest is the limiting behavior that occurs for higher average temperatures with respect to both the number of meals consumed and nutrient uptake into the hemolymph. The predicted number of meals consumed is identical for both 38 and 34° (Fig. 7c), but nutrient uptake is slightly higher for 38° (Fig. 7d). This is owed to the physiological advantage that an insect gains when operating in the "high risk" temperature region of the reaction curve. For the purpose of this paper, we define the high risk portion of the reaction curve to be the region to the right of the maximum (point A in Fig. 6). If it is assumed that an animal operates in a range of body temperatures (i.e. it is unable to maintain exact temperature homeostasis), then it can be easily verified analytically that for a standard development curve (Lactin and Johnson, 1998) it will achieve a physiological advantage if some of the temperature range includes the "high risk" region of the development curve. The disadvantage of operating to the right of the peak in a developmental curve is that an additional small increases in body temperature could potentially be fatal. The construction of a risk assessment model that explores the trade off between physiological gain and the additional risk incurred by operating in the high risk area is a direction of future research.

5.2. Conclusions

We have extended existing chemical reactor models and quantified feedback mechanisms that provide a connection between digestion and foraging. The compartmental, reactor model with feedbacks

captures much of the biological reality involved in these processes and gives key insights into nutrient acquisition and processing. The model shows that nutrient titers in the hemolymph can increase or decrease gustatory responsiveness. Thus, we have obtained a phenomenological model with dynamic feedbacks that leads to qualitative and quantitative predictions about grasshopper foraging behavior. The simulations of intermeal delays are consistent with other models and experiments that have been developed to describe grasshopper intermeal behavior (e.g., Simpson and Raubenheimer, 2000).

The model also shows the importance of temperature in modulating linkages between food acquisition and digestion. We note that the model was not effective in describing observed insect behavior until external temperature effects were included, thus emphasizing the importance of incorporating thermal regulation in insects. A model that ignores temperature may not be effective in explaining foraging behavior and digestion in grasshoppers. Although the inclusion of temperature leads to a problem that is less tractable analytically, it creates no difficulties when solving the model numerically.

In summary, the model developed here can provide an important, initial component to complement an experimental program designed to understand interconnections between ecological issues (foraging, food quality, temperature) and physiological issues (digestion and absorption). It points out that digestion, modified by temperature, is an important rate-limiting step in nutrient acquisition.

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