A CONCEPTUAL MODEL FOR GROWTH, DEVELOPMENT, AND REPRODUCTION IN THE LADYBIRD BEETLE, *HIPPODAMIA CONVERGENS* (COLEOPTERA: COCCINELLIDAE)[1]

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Abstract

A simple model for growth and development of the ladybird beetle (*Hippodamia convergens* G-M.) which partitions aphid biomass eaten into components of excretion, assimilation, growth and/or reproduction, and metabolic costs associated with searching and maintenance respiration is reported. All parameters in the model were estimated from simple *minimal* laboratory experiments, and have biological and/or physical meaning. The effects of predator nutrition on aging, survival, and emigration were also modelled. Most rates in the model for growth, reproduction, and respiration are controlled by the interplay between prey consumption and maximum prey biomass demands. The model for biomass flow is related to standard predator/prey theory.

INTRODUCTION

Many ecologists have been concerned with ecological energetics which is the science of assessing the flow of energy through ecological food chains, while others have focused attention at the organism level on the assimilation of consumed biomass or energy into components of growth reproduction, excretion, and respiration. A review of this literature is quite beyond the scope of this paper, but readers might well refer to the interesting collection of important papers on various aspects of this topic which have been assembled by Wiegert (1976). Simple energy flow dynamics models of ecological systems are common in ecological texts (see Odum 1971), but few workers have attempted to bring together all of the components of predation (cf. Holling 1966; Hagen and Sluss 1966; Fraser and Gilbert 1976; Tamaki *et al.* 1974) and biomass assimilation into one model (cf. Mukerji and LeRoux 1969; Rogers and Randolph 1978). Beddington *et al.* (1976*a*) (see also Hassell 1978) and Gutierrez *et al.* (1976) proposed preliminary models of this nature, but the model parameters were not clearly defined.

In this paper, a simple empirical model for biomass (energy) flow in the ladybird predator (*Hippodamia convergens* G-M.) is presented which describes its growth, reproduction, aging, survival, and migration rates in alfalfa (*Medicago sativa* L.). The larval and adult stages of the ladybird beetle are important predators of aphids in western North America (Hagen 1974; Neuenschwander *et al.* 1975; Fraser and Gilbert 1976). The proposed model is a special case of the Fraser–Gilbert (1976) functional response model.

MATERIALS AND METHODS

Diapausing adult beetles were collected during winter from overwintering sites in the Sierra Nevada mountains. The predation success of the adult beetles and their progeny was studied in arenas like the one shown in Fig. 1. Each arena consisted of a 24×24 cm plexiglass plate with eight equidistant small holes in the center. Cut stems of alfalfa 24 cm high were placed through the holes, which were 3.8 cm
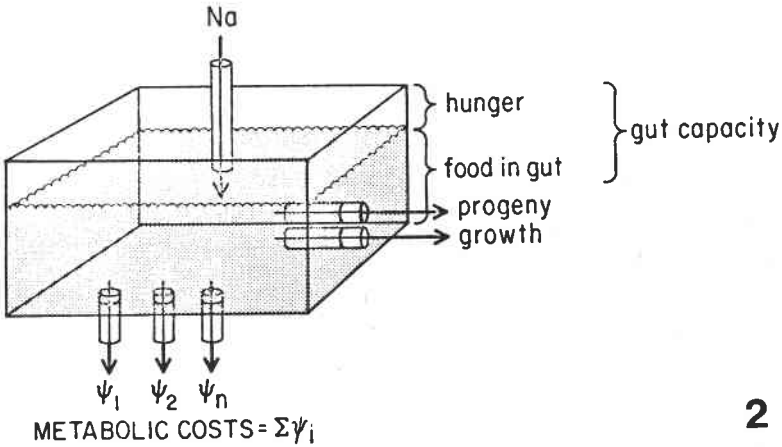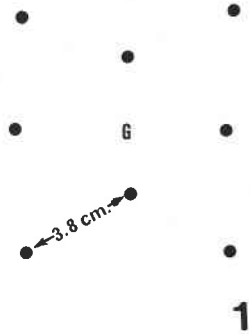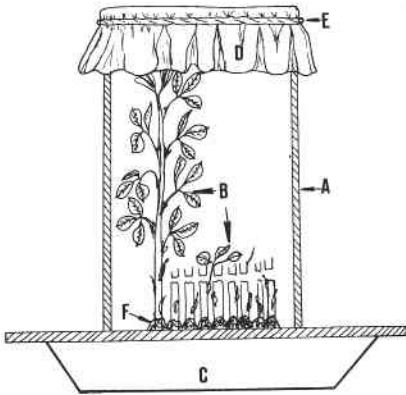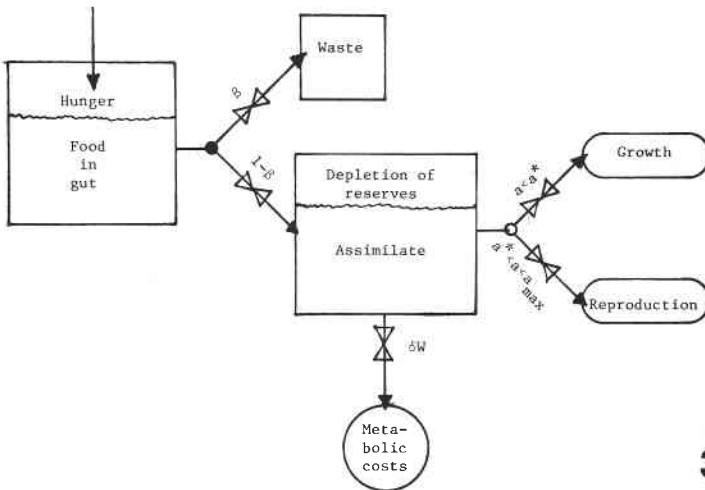
FIGS. 1-3. 1, the experimental arena: (A) plexiglass tube and plate, (B) 8 cut alfalfa stems, (C) shallow water-filled pan, (D) cheesecloth top, (E) rubber band, (F) putty, and (G) the spacing pattern of the stems. 2, the metabolic pool model for a generalized predator (cf. Gutierrez and Wang 1976). 3, a metabolic pool model for a generalized predator separating hunger from assimilate allocation.

apart, secured around the base with putty and the plate was placed over a shallow water-filled tray.

Specified numbers (usually 1, 3, or 5) of preweighed aphids were placed on each stem and a 15.8 cm diameter plexiglass cylinder coated on the inner surface with a nontoxic, slippery fluorocarbon aerosol spray was placed around the stems. The fluorocarbon spray prevented the beetle from fruitlessly searching the walls of the cylinder. A mated female beetle was introduced and the top of the cylinder sealed with an organdy square. Females were kept in the arena 24 h at 24.8°C under long light conditions (14–16 h), then removed for 1 h, mated in a 10 dr vial, and reintroduced into restocked arenas. Surviving aphids and all beetle eggs were removed and counted. This process was repeated over several days. Setting the experiments up was extremely time-consuming as the live weights of the beetles, their eggs, and the aphid prey were measured with a Cahn Electrobalance (±.01 mg). *This fact severely limited the number of replicates.*

Time (t) and age (a) in this paper are expressed in day-degrees (D°) above one developmental threshold of 8.8°C even though small differences in the thermal thresholds of the various life stages were found by Butler and Dickerson (1972) (see Table I). The durations of the different life stages are also shown in Table I. Estimating the various rates in the model per D° makes the model more general than using chronological time.

THE MODEL

The model originally proposed by Gutierrez and Wang (1976) is shown in Fig. 2, but it is inadequate because it has combined gross food intake with the process of assimilation. A better model is seen in Fig. 3 which separates the two. Hunger determines food demand, while metabolic needs determine assimilate requirements, but the two are linked.

Table I. A summary of the developmental thresholds and developmental times for the ladybird beetle (*Hippodamia convergens* G-M.) (see Butler and Dickerson 1972)

	Thresholds	
Instar	Threshold	D°
Egg	7.4°C	29.3
Larva	8.8°C	200.0[a]
Pupa	8.8°C	42.3
(prepupa not calculated)		

	Developmental time of beetles reared with maximum food		
Instar	Days at 21.1°C	D°>8.8°C	D° cumulative
Egg	3.05	29.3	29.3
L₁	4.01	49.3	78.3
L₂	2.57	31.6	110.0
L₃	3.08	37.7	147.7
L₄ + prepupa[b]	6.51	80.0	228.0
Pupa	3.48	42.3	270.8
Preova	5.52	67.9	337.7
Adult	61.46	756.0	1104.7

[a]Includes prepupa.
[b]Prepupa are always considered to be fourth instar larvae.

Hunger Model

The quantity of prey (Na) a predator eats during some period of time (Δt) is determined by its searching success which is conditioned by behavior and physiological state. The rate of search is greatly influenced by beetle size (W) and hunger (H_t). Hunger is defined here as

$$0 \leqslant H_{t+\Delta t} = \Omega_t - Na_t - F_t + E_t + \Delta\Omega_t \leqslant \Omega(W)_{max}. \qquad [1]$$

All variables defined below are expressed as mg of biomass.

Ω_t = gut capacity at time t

F = food in gut

E = food leaving gut via excretion and assimilation during Δt

Na = mg prey eaten = f (prey, predators, ·)

$\Delta\Omega$ = change in gut capacity during Δt only if the beetle is immature

$\Omega(W)_{max}$ = maximum gut capacity of the beetle = f(W)

W = mass of the beetle.

Laboratory experiments indicate that food eaten is processed within one day, hence the daily flow of Na into the gut is balanced by the outflows (i.e., excretion, assimilation, and metabolic costs). Hunger is a transitory state, and we ignored it in our model with little apparent effect. The influence of behavior on Na is incorporated in the search (A) and prey consumption demand (b) rates, which are related to predator size. The incorporation of A and b into the model is discussed in a later section. The hunger model is given only for historical reasons (see Holling 1966).

Assimilation Model

Of prey consumed, a fraction β is excreted, and $(1-\beta) \cdot$ Na is assimilated and/ or used to meet metabolic costs ($z\dot{W} \cdot \Delta$t) (Fig. 3). Growth and reproduction are age dependent (i.e., only immatures grow and only mature adults produce eggs). In the model, the first priority of assimilate use is maintenance respiration ($zW \cdot \Delta$t), then growth (ΔG) and reproduction (ΔR). The model for the assimilation of Na into ΔW is

$$\Delta W = [Na_t(1-\beta) - z(W_t + \tfrac{1}{2}\Delta W)\Delta t]$$
$$\Delta W [1 + \tfrac{1}{2}z\Delta t] = [Na_t (1-\beta) - zW_t\Delta t] \qquad [2]$$
$$\Delta W = \frac{Na_t (1-\beta) - zW_t\Delta t}{1 + \tfrac{1}{2}z\Delta t} \simeq [Na_t (1-\beta) - zW_t\Delta t] [1 - \tfrac{1}{2}\Delta t]$$

i.e., $\Delta W \simeq$ assimilate $-$ (metabolic costs of W + ΔW)

where ΔW = growth (ΔG) or reproduction (ΔR) increment during Δt (i.e. $16D°$)

z = respiration rate

β = excretion rate.

But as $\Delta t \to 0$, $Na_t = k_t\Delta t$ and $\Delta W = k_t (1-\beta)\Delta t - zW_t\Delta t$ (see derivations of Na in [5]). Note that Δt in our study was $16D°$. Only the parameters z (mg/mg/D°) and β need be roughly estimated.

Estimating maintenance respiration rate (z). Fully fed females given free water were starved at room temperature and weighed at regular intervals to determine their weight loss. The first day (t_1), the gut empties and the weight changes rapidly, while on subsequent days the rate of change is constant and equals $\hat{z}$ per day (e.g., Fig. 4). The average fraction body weight loss per beetle per day was estimated from t_2 to t_4 and equals $\hat{z} = 1 - (\overline{W}_{t+1}/\overline{W}_t)$. $\hat{z}$ is the maximum rate because the starved beetles were searching at their maximum rate. The beetles use body fat and
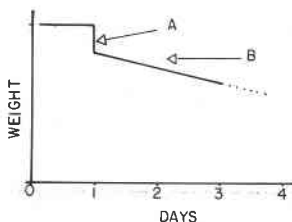
FIG. 4. A schematic model of weight change of starved beetles: (A) rapid drop in weight caused by emptying of the gut, and (B) the gradual loss of weight due to the utilization of body fat.

other body tissues to meet basic maintenance costs, but we have not attempted to correct for caloric values in the model. As we shall see, the model remains reasonably robust despite this shortcoming, and the small sample size.

In the first experiment, $\hat{z}$ equalled 0.089 ± 0.02 ($n = 4$), and all females died by time $t = 3^1/_2$, after utilizing 22.0% of their total body weight. In two other experiments $\hat{z}$ equalled 0.074 ± 0.029 ($n = 7$) and 0.081 ± 0.042 ($n = 13$) but were not significantly different from that reported above. For males $\hat{z}$ was 41% less. Thus, the weighted average maximum rate per D° for females ($\hat{z}_{max} = 0.080/16D^\circ$) is 0.0050, but decreases as $Na/bW\Delta t \to 1$ (see [3]), where b is maximum demand for prey per mg of predator per D°.

$$0.0040 \leq z_{max} (1 - 0.2\ Na/bW\Delta t) < 0.0050. \qquad [3]$$

The coefficient (0.2) in [3] was estimated from unpublished searching behavior data, which shows that the area searched by fully fed beetles is 80% that of starved beetles. The prey demand rate (b) and Na are derived in subsequent sections.

Estimating excretion rate (β). If Na is the prey biomass eaten during Δt, $zW \cdot \Delta t$ the maintenance cost, and ΔW the change in weight, then we can solve [2] for β:

$$\beta = (Na - zW \cdot \Delta t - \Delta W/(1 - z\Delta))/Na$$

$$\qquad [4]$$

$$\beta = wastes/Na.$$

All of the variables were measured in an independent experiment, and z was estimated above. Six ovipositing adult females were given eight 1.5 mg aphids per day for a 9.25 day period at 24.8°C, and the changes in weight and numbers of eggs deposited determined. The average daily values (mg) were substituted in [2]

$$\overline{\Delta G} + \overline{\Delta R} = (Na - \beta \cdot \overline{Na} - \hat{z}\overline{W}_t)\ (1 - \hat{z})$$

where $\hat{z} = 0.080$ per day, $\overline{Na} = 9.5$, $\overline{W} = 22.8$, $\overline{\Delta G} = 0.29$, and $\overline{\Delta R} = 0.13$ and $\Delta t = 1$ day. Substituting the values yields $\beta = 0.74$. ΔR was estimated by multiplying the number of eggs by their average mass (i.e., 0.22 ± 0.05 mg, $n = 36$). Note that not all of the aphids were found each day, and β is not independent of $\hat{z}$, but the model is qualitatively tested against independent data in a later section.

The Functional Response

Prey consumption (Na). All of the above discussion presupposes that we know the searching success (Na) of beetles [2]. This is clearly not the case. Many predation submodels for estimating Na have been proposed (see Lotka 1925, Volterra 1926, Nicholson 1933, Holling 1965, and Royama 1971), but only that proposed by Fraser and Gilbert (1976) was developed from laboratory and field experiments and was field tested. Gutierrez and Wang (1976) analyzed some of the theoretical properties of the Fraser–Gilbert model (1976) (eq. [5])

$$Na = N_c f(N,M,W,P) = N_c M[1 - e^{(-bWPT/N_c M)(1 - e^{(-AN_c M/b)})}] \qquad (i)$$

and $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ [5]

$$Na = k_t \Delta t = bWP\Delta t[1 - e^{(-AN_c M/b)}] \qquad (ii)$$

All variables have been defined above except:

N_c = the corrected number of prey available (see Gutierrez *et al.* 1980)

P = predator numbers $(1 < P < \infty)$

$T = \Delta t$ = increment of time in physiological units (i.e., day-degree)

M = mg/prey

b = predator demand rate (mg prey/mg predator/D°)

A = the predator search rate (g(b)) (i.e., stems searched/D°).

The Lotka–Volterra and Nicholson–Bailey models are but special cases of the Fraser–Gilbert model. This deterministic model [5] describes the searching success of the individual $(P = 1)$ or on average for the population $(P > 1)$.

This fact marks an important transition point, as all prior discussion concerned individual predators. In the model, the quantity of prey captured (Na) may be expressed in terms of energy, mass, or numbers. In our study only the latter two were of interest. Only the predator demand rate (b) and search rate (A) have not been derived.

Prey demand rate (b) per predator. Beetle larvae $(n > 75)$ have some average potential maximum growth rate (v^*) which is a function of body mass and temperature. Figure 5 plots average net weight gain of more than 75 beetles from egg hatch to pupation under condition of unlimited food during each of the instars against the weight at the beginning of the instar. The slope $(v^* = 1.75)$ is the observed rate of growth per life stage. We can now use the model to work backwards to estimate b. Previous studies indicate that 24% of the prey eaten is available for assimilation (8.0% for maintenance costs and 16.0% incorporated biomass at 24.8°C). Logically one can estimate that the assimilate demand $(\Delta \hat{b})$ per life stage (Δt^*) as

$$\Delta \hat{b} = [v^* W(1 + z\Delta t^*/2) + zW \cdot \Delta t^*] \qquad [6]$$

where 1.75 $W(1 + z\Delta t^*/2)$ is both the growth increment and the average maintenance cost during Δt^*, while $zW \cdot \Delta t^*$ is the maintenance cost of the initial mass. To estimate $\hat{b}$ we divided [6] by the average length of the active parts of the larval life stages $(\Delta t^* = 39D°)$, and multiply by $\gamma = \beta/(1 - \beta)$ to correct for excretion. This linear estimate of b in the model resulted in excessive growth, due to the fact that the estimate of growth $(v = v^*/\Delta t^* = 0.045)$ per day-degree was too rough an approximation. A better model is to assume that the beetle grows exponentially from t to $t + \Delta t^*$, hence $W_{t+\Delta t^*} = W_{t_0} e^{v\Delta t}$, where $W_{t+\Delta t^*} = W_t + 1.75 W_t$ and v in this case is the instantaneous growth rate.

$$v = \log_e(\frac{W_{t+\Delta t^*}}{W_{t_0}})/\Delta t^* = \log_e(2.75)/39D° = 0.0259.$$

Substituting $ve^{v(t-t_0)} = ve^{v\Delta t}$ in [6], taking $\Delta t = 1$ and multiplying by γ yields

$$b = \gamma[ve^v W(1 + z/2) + zW]. \qquad [7]$$

This estimate for total demand (b), which equals assimilate plus excretion demand rate, is highly satisfactory. Note that demand depends upon weight, not age.

Rate of search (A). Laboratory studies indicate that A is greatly influenced by weight and hunger. If we ignore hunger *per se*, and use b as a surrogate, we define the search rate as follows:

$$A_t = A_0 * b_t/b_0 \qquad [8]$$

where A_0 is the search rate of a newly hatched larva (i.e., the stems searched/ (number of stems available $\times \Delta t$) = 0.0078)), and b_0 and b_t are the prey demand rates of a newly hatched larva and a larva at its current growth state (see derivation of b). Hence we see that b which is a measure of hunger and A which is greatly influenced by hunger are intimately linked.

The Metabolic Pool Model

Metabolic pool priority scheme. The priority scheme for allocating assimilate growth and reproduction is similar to that proposed for cotton by Gutierrez and Wang (1976).

$$(i) \text{ if } \Delta W > 0 \begin{cases} \Delta G = \Delta W \text{ if } a < a^* \\ \begin{cases} \Delta R = \Delta W \text{ if } a \geqslant a^* \text{ and } W_t \geqslant W_{max} \quad (\text{see } iii) \\ \Delta G = \Delta W \text{ if } a \geqslant a^* \text{ but } W_t < W_{max} \end{cases} \end{cases}$$

where a = age in $D°$, $a^* = 337D°$ is the minimum age at repro-   [9] duction, W_{max} is the maximum prior mass achieved and the number of eggs produced equals ΔR/(mass of one egg = 0.22 mg).

(ii) if $\Delta W = 0$, then $\Delta G = \Delta R = 0$.

(iii) if $\Delta W < 0$, then $\Delta G = \Delta W$, $\Delta R = 0$ and $0.8 W_{max} \leqslant W_{t+\Delta t} = W_t + \Delta W$. In the model the beetles are assumed to have used all of their reserves and die when weight loss is greater than $0.2 W_{max}$. The threshold comes from our small experiment to estimate z (see above).

The costs of converting prey tissues (Na) to predator tissues (G, R) are included in β and not in z which measures only maintenance respiration. *For simplicity*, we assume ΔG and ΔR accrue via the same process, but the allocation is age-dependent as immatures increase in body size, while reproductive adults produce eggs. In general, nondiapause beetles do not have large fat reserves.

A Test of the Assimilation Model

The model [2] was tested against an independent set of oviposition data ($n = 20$) in Fig. 6. These data represent the results of three experiments wherein female beetles of various sizes were allowed to search for 1, 3, and 5 aphids per stem in the experimental arena. The mass of the aphids and predators before and after the experiment was measured. The dashed line excludes maintenance costs for the growth increment, while the solid line includes them and yields a reasonable fit to the data. This is extremely pleasing as the model parameters were estimated from minimum experiments. The x-intercept (0.35 approx.) estimates the compensation point for the predators ($Na(1-\beta) = zW\Delta t$). Furthermore, z_{max} can be estimated from the data by assuming that we have a 20 mg beetle which requires 7.0 mg prey (i.e., $20 \times .35$) for basic maintenance respiration. Thus, if 24% of the 7.0 mg is assimilated (1.68 mg), the respiration rate is 0.084 per day. This is very close to the 0.080 computed in a prior section.

Modelling Other Effects of Nutrition

It is well known that partially starved insects require longer to complete each life stage and their mortality rates increase accordingly.

Aging. The influence of different levels of constant food (mg/mg) on the adult preoviposition period is seen to be a decreasing function of mg prey/mg predator
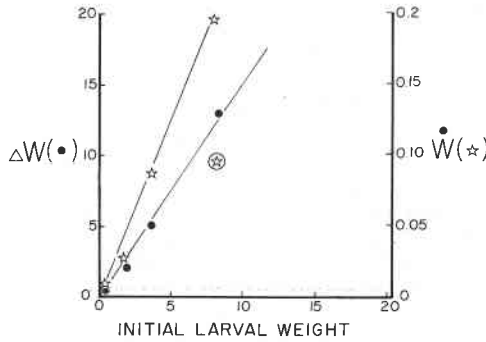
FIG. 5. The relationship between weight gain (ΔW) and the rate of gain ($\dot{W}$) per life stage on the initial weight at the beginning of each life stage. $\dot{W}$ for fourth instar larvae was corrected for the fact that the length of the stage as measured also included a quiescent period (i.e., ⊛).

(Fig. 7A), while 7B shows the effect of increased variability of daily food intake ($S/\overline{X}$ of mg/mg) on the preoviposition period. Only experiments with more than three individuals were used to compute $S/\overline{X}$ values which explains the difference in the number of data points in 7B. Much of the scatter in the data results from the highly variable daily consumption rates caused by the uneven searching success of the beetles.

In the model, beetle eggs hatch at a = 29D°, and on average during each Δt accumulate age in increments of Δa. The maximum value of Δa is determined by temperature, but $\Delta t \neq \Delta a$, because the actual accrued age must also be modified by some measure of the beetles' nutritional state (ϕ), which in this model is the ratio of food eaten (Na) to the prey mass required to meet maximum demands for growth, reproduction, and metabolic costs (i.e., $bW\Delta t$). Equation [10] formulates this notion.

$$a_{t+\Delta t} = a_t + \Delta a \cdot \phi, \text{ where } 0 \leq \phi = Na/(bPW\Delta t) < 1 \qquad [10]$$

and substituting [5ii] for Na yields $\phi = [1 - e^{-ANM/b}]$ if Δt is very small.

Mortality. The probability of survival (S) during Δt for individuals or on average for the population can be modelled as

$$0 \leq S_t = \alpha + (1 - \alpha) Na/(0.8bPW\Delta t) \leq 1. \qquad [11]$$

The coefficient 0.8 was estimated from computer simulations. The starvation experiments show that most fully fed beetles die within 4 days when food is withheld
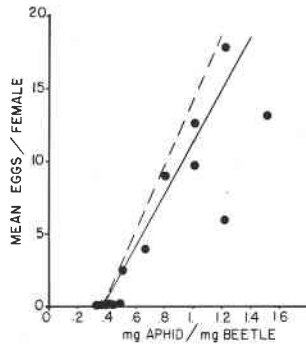

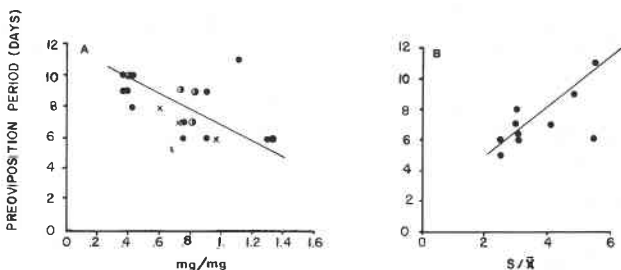FIG. 6. The mean number of eggs produced per 16D° > 8.8°C by female ladybird beetles fed varying mg of aphids/mg of body weight.

FIG. 7. The influence of mg aphid/mg beetle on (A) the preoviposition time in days (16D°/day) of females, and (B) the influence of the variability of prey consumption ($S_{mg/mg}/\bar{X}_{mg/mg}$) on preoviposition time. The different symbols in A represent different experiments.

because they have depleted their reserves (i.e., $W_t = 0.8W_{max,t-4}$). If beetles are starved (i.e., Na = 0), $\alpha = 0.5$ is the estimated probability of survival during $\Delta t(16D°)$, hence the probability of surviving 4 days is

$$\prod_{i=1}^{4} S_i = 0.5^4 = 0.0625. \qquad [12]$$

In view of the estimation error involved in the experiment, α appears to be quite reasonable. Furthermore, as Na $\rightarrow 0.8$ bPW·Δt, S $\rightarrow 1$, but as we shall see in the next section, Na is always less than 0.8 bPWΔt because searching success is imperfect. Figure 8 (I and II) depicts the two extremes of survivorship predicted by [11] (fully fed and starved), while III shows an intermediate pattern.

Emigration. Adult beetles, but not larvae, emigrate from the fields when prey densities are low. The probability E that an adult beetle emigrates from the field is assumed to be a function of prey supply–demand.

$$0 < E_t = Na/bPW\Delta t < 1. \qquad [13]$$

This fits well with field observations of Hagen and Sluss (1966) who noted that on average 1 mg of aphids per alfalfa stem was required to keep adult beetles in the field and to begin reproduction. This quantity of aphids is approximately equal to the .35 mg prey/mg predator predicted by the model as the metabolic compensation point (i.e., $Na(1-\beta) = zW\Delta t$).

Immigration. Estimating immigration (IM) is a more difficult problem because the population (P*) surrounding the study field is unknown, and the attraction rate of individual fields is likewise unknown. The model for immigration should be some function ($0 \leq IM_t = g(Na/bPW\Delta t \leq 1$) of food availability, but further work is required before it can be formulated.

Simulation of Individual Predator Growth and Development

Simulation results for individual beetles are presented here, while those describing the population dynamics of the alfalfa plant, pea aphid (*Acyrthosiphon*
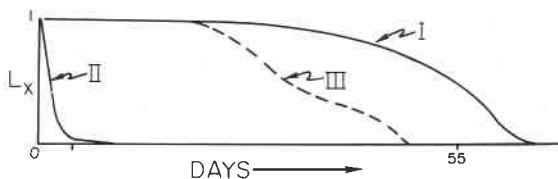

FIG. 8. Predator survival under conditions of varying food: (I) maximum food, (II) minimum food, and (III) variable food.

pisum Harris) and blue alfalfa aphid (*A. kondoi* Shinji) and *H. convergens* are described elsewhere (Gutierrez *et al.* 1980).

Figure 9 shows the simulated growth and development of a newly hatched larva in our experimental arena under the conditions of 1, 3, or 5 aphids per stem at a constant temperature of 24.8°C. The results (9A) show that the aging rate (time to reproduction) slows, while growth and fecundity decrease as food supply/demand decreases. Figure 9B, C shows the effects of beetle nutrition on fecundity and developmental time. Data on the effects of feeding on oviposition are shown in Fig. 6 (vs. 9B), while the effects of nutrition on the preoviposition times of adults can be compared in Fig. 7A (vs. 9A).

The effects of nutrition on aging from egg hatch to first egg can be seen by comparing the Butler–Hamilton data in Table I (at 21°C) with the simulation (9A at 24.8°C). Converting both estimates to the same time units (D°) shows that 308D° in Table I compares well with the 336D° (approximately) predicted by the simulation at 5 aphids/stem. The Butler–Hamilton experiments did not require that the beetle search for food, hence prey demand would be expected to be smaller and the aging rate slightly faster. The results should nonetheless be viewed as qualitative. The simulated effects of food on survivorship (9D) cannot be tested because of insufficient data. Experiments are now under way to rectify this deficiency.

The model, while relatively simple, yields a very rich dynamic behavior which is also reasonably realistic. We have resisted the temptation to add the complexities of caloric content of tissues, stochasticity of variables, and more subtle aspects of beetle behavior. The attempt has been to describe the influence of feeding on different aspects of the beetle's biology.

DISCUSSION

At the level of the individual, the major facets of predator growth and development have been incorporated into a simple model [2], vaguely similar to that
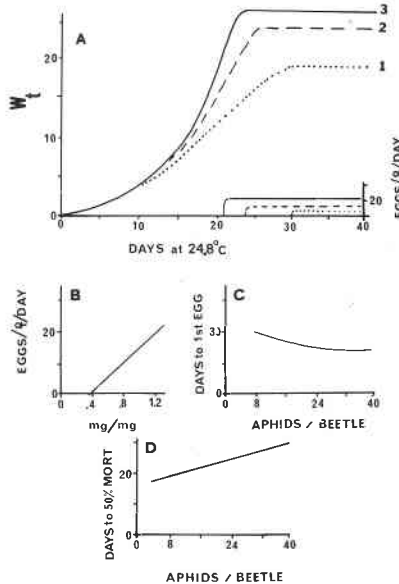

Fig. 9. The simulated effects on (A) growth, (A,B) fecundity, (C) devleopmental time, and (D) survivorship of exposing ladybird beetle larvae from egg hatch for a 50 day period at 24.8°C (Δt = 16D°) to 1, 3, and 5 one mg aphids on each of eight stems (8, 24, and 40 aphids).
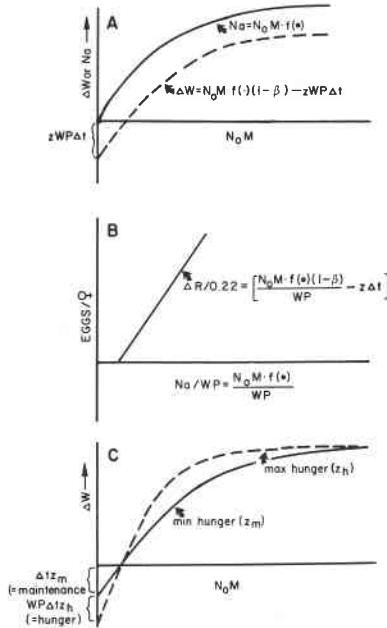
FIG. 10. A generalized net growth function for predators: (A) with (- - -) and without (——) incorporating metabolic costs due to maintenance respiration (z) and losses due to excretion (β); (B) the production of eggs/female as a function of mg prey/mg predator; and (C) (9A) with the inclusion of hunger on increased maintenance respiration. All variables are defined in the text.

described by Schoener (1973). This model was an outgrowth of a field metabolic pool model for allocating photosynthate to plant parts developed by Gutierrez *et al.* (1975), Gutierrez and Wang (1976), and Wang *et al.* (1977). That model showed how the interplay of photosynthate supply and demand controlled growth and development processes in single plants or plant populations, and in this case how prey supply affects the growth and development of a predator (or herbivore). The model (eq. [2]) can be rewritten for completeness, ignoring the metabolic costs of the growth increment as

$$\Delta W = N_0 M \cdot f(N,M,P,W)(1-\beta) - zPW\Delta t \qquad [14]$$

where $1 < P < \infty$, and $f(\cdot)$ is a predator functional response model through the origin (i.e., the Fraser–Gilbert model in this case (Fig. 10A, the solid line)). The model is a type II functional response (Holling 1966). Subtracting the metabolic costs (y intercept $= zPW\Delta t$) shifts the curve to the right and the correction for excretion $(1-\beta)$ lowers it. The curves saturate at high prey density, because predator demands ($bPW\Delta t$) are met asymptotically. Similar but less analytical models were developed by Gutierrez *et al.* (1976), Gutierrez and Wang (1976), Beddington *et al.* (1976b), and later by Readshaw and Cuff (in press) who modelled A. J. Nicholson's blowfly data from a more realistic perspective. Note above that both the demand (b) and the search (A) rates in $f(\cdot)$ are variables. If we assume an adult beetle, and $N_a \rightarrow N_0$, then dividing N_0 by WP and $\Delta W = \Delta R$ by 0.22 mg yields the functions shown in Figs. 10B and 6. Hunger increases searching costs (z_h) and these must be added to basic maintenance (z_m) costs (i.e., $z_t = z_m + z_h$). These costs are incorporated in $f(\cdot)$ via the parameters b and A. These added costs are reflected in Fig. 10C as an increase in the slope of the function. Hunger associated

behavior in a population (i.e., emigration) transforms [14] to a type III functional response.

The net predator growth function (Fig. 10A,- - -) is analogous to a standard net photosynthesis function (Thornley 1977, Chap. 4), which brings the argument full circle: animal demographic equations (Von Foerster 1959) have been used to model plant populations (Gutierrez and Wang 1976), and a heretofore plant metabolite allocation model (Gutierrez *et al*. 1974; Gutierrez *et al*. 1975; Wang *et al*. 1977) has been modified to describe changes in predator growth and development, adult fecundity, aging, survivorship, and emigration rates at both the individual ($P = 1$) and the population level ($P > 1$).

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