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Reviewed work(s):

Source: *Ecology*, Vol. 73, No. 5 (Oct., 1992), pp. 1552-1563

Published by: [Ecological Society of America](#)

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# PHYSIOLOGICAL BASIS OF RATIO-DEPENDENT PREDATOR–PREY THEORY: THE METABOLIC POOL MODEL AS A PARADIGM<sup>1</sup>

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**Abstract.** Ratio-dependent models of predators and prey are approximations of the biology of resource acquisition and allocation and their consequences for population birth and death rates. A demand-driven functional response model that has a physiological basis in mass (energy) dynamics is reviewed (i.e., the metabolic pool model), and its obvious links to the logistic model are outlined.

To demonstrate the utility of this approach, a distributed maturation time age-structure model of the dynamics of A. J. Nicholson's classic laboratory population data on the sheep blow fly (*Lucilia cuprina* Weidman) is developed. The model provides sufficient information on the dynamics of the intermediate life stages to show that the blow fly oscillations were due to the effects of larval competition for food on size, fecundity, and pupation success. These results agree with Nicholson's conclusions. The advantage of this model, in contrast to prior models, is that the dynamics emerge by considering the processes of resource acquisition and allocation as they affect growth, reproduction, and survival. No explicit time delays, which automatically lead to oscillations, were included. Lastly, the notions of the metabolic pool model are found in Nicholson's original model for equilibrium population density.

The metabolic pool paradigm in an age-structure setting is used to model the tri-trophic dynamics of *Acyrtosiphon* aphids in an alfalfa ecosystem. The model explains the role of the various natural enemies in the regulation of the aphids.

**Key words:** age-structured delayed-maturation time model; blow fly; multi-trophic models; physiological basis ratio-dependent predator–prey model; population dynamics.

## INTRODUCTION

Conventional wisdom assumes that the behavior of a predator is driven in large part by demands for resources, including food for respiration, growth, and reproduction. However, the biological details are mostly excluded from population dynamics models. General first-order differential equations are often used to describe simple Lotka-Volterra type prey–predator dynamics:

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(N,P)P \\ \frac{dP}{dt} &= hg(N,P)P - \mu P,\end{aligned}\quad (1)$$

where  $f(N)$  is the per-capita prey birth rate ( $N$ ),  $g(N,P)$  is the predator ( $P$ ) per-capita consumption rate of prey,  $h$  converts prey eaten to predator offspring, and  $\mu$  is the per-capita predator death rate (e.g., Arditi and Ginzburg 1989). The biology of trophic interactions is subsumed in  $f$ ,  $g$ ,  $h$ , and  $\mu$  in simple dynamics models.

Lotka's (1925) original model was based on mass (energy) units, and the convertibility of mass and number units has been assumed in the literature, and will be exploited here.

Ratio-dependent theory of prey–predator interactions assumes that per-capita functional response mod-

els of the form  $g\left(\frac{N}{P}\right)$  are more suitable than are  $g(N)$

or  $g(N,P)$ . This idea has been in the literature for decades (e.g., Thompson 1939, Leslie 1948, Frazer and Gilbert 1976, Gutierrez and Wang 1976, Berryman 1981, Gutierrez et al. 1981, Berryman and Stenseth 1984, Getz 1984, Arditi and Ginzburg 1989, Arditi et al. 1991), and its physiological basis has been partially outlined. In this paper, the physiological basis for ratio-dependent theory is developed and a per-capita model is described that includes the relevant biology without adding undue complication. Eq. 1 and its elements are modified in successive steps to show this process.

Mass ratio-dependent models of form  $g\left(\frac{M_i}{M_{i+1}}\right)$  may

<sup>1</sup> For reprints of this Special Feature, see footnote 1, p. 1529.

be used for both predator ( $M_{i+1}$ ) and prey ( $M_i$ ) masses, and the trophic interactions (Eqs. 1) may be rewritten as follows:

$$\begin{aligned}\frac{dM_i}{dt} &= f\left(\frac{M_{i-1}}{M_i}\right)M_i - g\left(\frac{M_i}{M_{i+1}}\right)M_{i+1} \\ \frac{dM_{i+1}}{dt} &= hg\left(\frac{M_i}{M_{i+1}}\right)M_{i+1} - \mu M_{i+1},\end{aligned}\quad (2)$$

where  $f$ ,  $g$ ,  $h$ , and  $\mu$  in Eqs. 2 are now in mass units and  $M_{i-1}$  is the prey's resource base (Gutierrez and Baumgaertner 1984). This model makes predator fecundity and prey mortality functions of the mass acquisition rate, but it does not resolve the issue of time-varying changes in average size (quality) of individuals. In general large predators require more food than small ones, and hence these differences have important effects on resource acquisition rates and on trophic interactions and dynamics. This suggests that the mass and number dynamics must be linked and the ratio-dependent functional response model must reflect the size dependence of per-capita demand dynamics. The linkage between prey mass ( $M_i$ ) and number ( $N$ ) dynamics is easily accomplished (Eqs. 3):

$$\begin{aligned}\frac{dM_i}{dt} &= h_i f\left(\frac{M_{i-1}}{M_i}\right)N - g\left(\frac{M_i}{M_{i+1}}\right)P \\ \frac{dN}{dt} &= q_i \left[\frac{dM_i}{dt}\right],\end{aligned}\quad (3i)$$

and for predator mass ( $M_{i+1}$ ) and numbers ( $P$ )

$$\begin{aligned}\frac{dM_{i+1}}{dt} &= h_{i+1} g\left(\frac{M_i}{M_{i+1}}\right)P - \mu M_{i+1} \\ \frac{dP}{dt} &= q_{i+1} \left[\frac{dM_{i+1}}{dt}\right].\end{aligned}\quad (3ii)$$

Here  $f$  and  $g$  are refined as per-capita mass-dependent acquisition functions,  $h_i$  and  $h_{i+1}$  are conversion coefficients in trophic levels  $i$  and  $i+1$ , and the constants  $q_i$  and  $q_{i+1}$  convert mass to numbers. This model assumes constant average size of prey and predators, and this can be resolved only by including the biology of resource acquisition and allocation in Eq. 3. To do this, the properties of the ratio-dependent model are developed from first principles.

#### THE PHYSIOLOGICAL BASES OF A RATIO-DEPENDENT MODEL

##### *The metabolic pool model for resource allocation*

The study of energy acquisition and allocation has a special terminology (Phillipson 1966, Petruszewicz and MacFayden 1970, Llewellyn 1988), which I will

simplify. The per capita metabolic pool model shown in Fig. 1a depicts the nutrient acquisition rate ( $M^*$ ) at time  $t$  for an individual ( $N$ ) of mass ( $M_i$ ) as well as the priorities for allocation (i.e., the levels). Resources consumed are partitioned in sequence to egestion ( $1 - \beta$ ), respiration ( $z$ , i.e.,  $Q_{10}$  for poikilotherms), costs of conversion of prey to predator ( $\lambda$ ) with the remainder assimilated ( $A$ ) to growth and reserves ( $G$ ) and/or reproduction ( $R$ ) (Gutierrez et al. 1981). This is part of the biology that is subsumed in  $h$  in Eqs. 1, 3. The feeding and assimilation rates of an individual ( $N = 1$ ) of mass  $M_i$  at time  $t$  and age  $a$  in trophic level ( $i$ ) varies depending on resource ( $M_{i-1}$ ) availability, and may be represented mathematically as follows:

$$A(t, a) = G(t, a) + R(t, a) = \{\beta M^*(t)N - zM_i(t)\} \lambda, \quad (4i)$$

or substituting  $f$  for  $M^*$  in Eq. 4i, yield

$$A(t, a) = \left\{ \beta f\left(\frac{M_{i-1}(t)}{M_i(t)}\right)N - zM_i(t) \right\} \lambda.$$

Species have characteristic assimilation (growth and reproduction) rate that may vary with age. Under non-limiting conditions, the observed feeding rate  $M^*$  in Eq. 4i is approximately the genetic maximum per capita demand rate ( $b[M_i, t]$ ) for food of an individual of mass  $M_i(t)$  at time  $t$  as follows (variables  $t$  and  $a$  omitted):

$$b \approx M^* = \frac{\frac{A}{\lambda} + zM_i}{\beta}, \quad (4ii)$$

In the model,  $A$  is always assumed to be the maximum rate (i.e., what it wants), but size  $M_i$  may vary considerably (i.e., a reflection of what it got in the past). Thus the function  $b = b(\cdot)$  defines what an organism is seeking at time  $t$  and is a prime motivator of search behavior (Gutierrez et al. 1981, Gutierrez and Baumgaertner 1984, Baumgaertner and Delucchi 1987). If  $M^* \approx b$  for all  $a$ , then the organism attains maximum size and has maximum fecundity (and longevity) (Gutierrez et al. 1981). Shortfalls in resource acquisition may be estimated by the ratio of supply acquired to the genetic demand (i.e.,  $0 \leq \phi(t) = M^*/b < 1$ ).  $\phi$  is always less than unity because search is imperfect even under nonlimiting conditions. Note that  $\phi$  is a function because  $M^*$  and  $b$  are time-varying. It is now imperative to select a functional response model that includes this physiology and the concept of search.

##### *The functional response model for resource acquisition*

A useful ratio-dependent model for predicting attack rates that has both demand and search components is

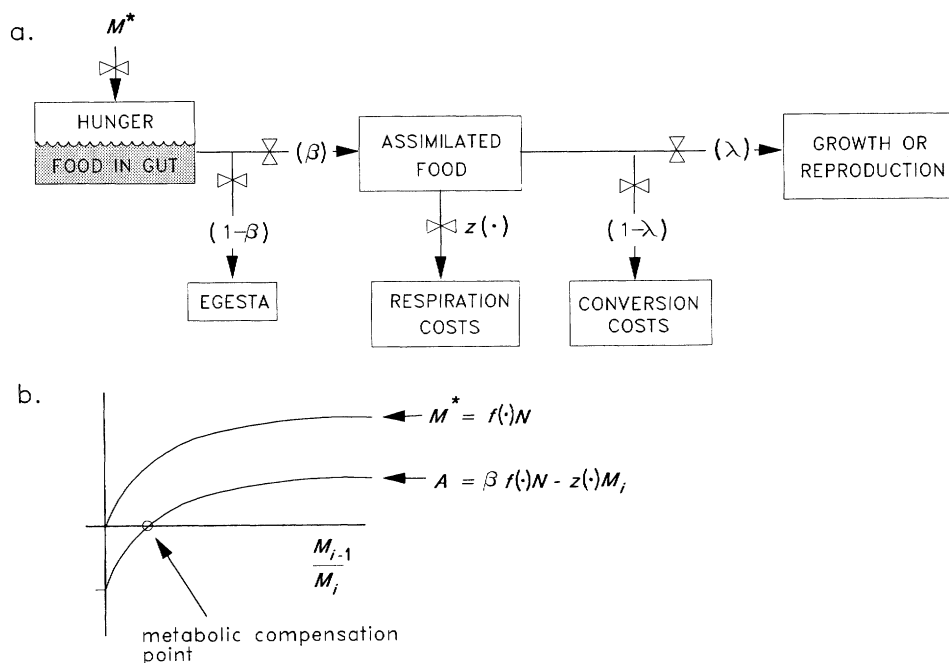


FIG. 1. The per-capita metabolic pool model of a predator ( $N = 1$ ) of average mass  $M_i$  and age  $a$  at time  $t$  in trophic level  $i$  feeding on a population of prey of total mass  $M_{i-1}$  in trophic level  $i-1$  (after Gutierrez and Wang 1976, and Baumgaertner and Delucchi 1987): (a) the per-capita energy acquisition ( $M^*$ ) and allocation ( $A$ ) rates with partitioning to egesta ( $1 - \beta$ ), respiration ( $z$ ) and conversion efficiency ( $\lambda$ ), and (b) the functional response with and without the metabolic costs subtracted.

the parasitoid model proposed by Frazer and Gilbert (1976; F-G). This model is a general form of the Nicholson and Bailey (1935) (N-B) and Lotka-Volterra (L-V) models (Gutierrez and Wang 1976). The F-G model has a predator form (Gutierrez et al. 1981 (G-B, Eq. 5), Klay 1987, see Royama 1971), which for our pur-

pose may be written as per-capita mass consumption in the  $i^{\text{th}}$  level as

$$M^*(t) = b_i(t) \left[ 1 - e^{-\frac{s_i M_{i-1}(t)}{b_i(t)}} \right]. \quad (5)$$

Again  $M^*$  is the mass of prey ( $M_{i-1}$ ) eaten per predator at time  $t$ , the function  $b$  is the maximum per-capita demand rate defined by (Eq. 4ii) in units  $M_{i-1}/N$ , and  $s$  is the Nicholsonian per-capita search rate expressed as the proportion of area searched per  $N$ . As defined above,  $b$  estimates the maximum demand rate assuming maximum  $A$  and the current state of  $M_i$ . Of course  $s$  may vary with organism size and changes in the search universe (Gutierrez and Wang 1976, Gutierrez et al. 1988, O'Neil 1989), but for simplicity  $s$  is assumed constant. Lastly, the units in the exponent cancel, resulting in a dimensionless number.

The model is concave on  $M_{i-1}/M_i$  (Fig. 2), suggesting that as per-capita prey abundance increases, the attack rate  $M^*$  saturates monotonically to  $b$ , which is a function of  $M_i$ . A Taylor expansion of Eq. 5 shows that the model becomes the L-V interaction term  $sM_{i-1}$  at low prey density (see Gutierrez and Wang 1976). These are the characteristics of ratio dependence outlined by Getz (1984). The task then is to incorporate this physiology into a population dynamics model. The first model examined lacks age structure.

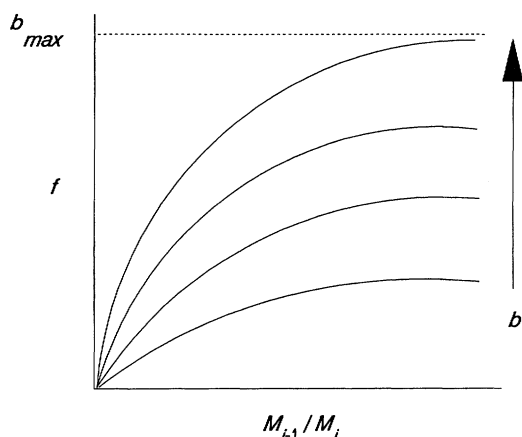


FIG. 2. An interpretation of the Gutierrez-Baumgaertner functional model ( $f$ ), where  $b$  is the per-capita resource demand rate of a predator of average mass  $M_i$  searching for prey of total mass  $M_{i-1}$ . Note that  $b_{max}$  is the maximum per-capita prey consumption rate.

*Incorporating the metabolic pool model into the dynamics model*

The linked mass and number dynamics models Eqs. 3i, ii) can be rewritten where  $h_i$  in Eq. 3i is replaced by the biology of resource acquisition and allocation (after Gutierrez and Baumgaertner 1984). The models for prey mass ( $M_i$ ) and numbers ( $N$ ) are

$$\begin{aligned} \frac{dM_i}{dt} &= \{\beta_i f(\cdot)N - z_i M_i\} \lambda_i - g(\cdot)P \\ &= \left\{ \beta_i \left[ b_i \left( 1 - e^{-\frac{-s M_{i+1}}{b_i}} \right) \right] N - z_i M_i \right\} \lambda_i \\ &\quad - \left[ b_{i+1} \left( 1 - e^{-\frac{s_{i+1} M_i}{b_{i+1}}} \right) \right] P \end{aligned} \quad (6i)$$

and

$$\frac{dN}{dt} = \phi_i q_i \left[ \frac{dM_i}{dt} \right],$$

and predator mass ( $M_{i+1}$ ) and numbers ( $P$ )

$$\begin{aligned} \frac{dM_{i+1}}{dt} &= \{\beta_{i+1} g(\cdot)P - z_{i+1} M_{i+1}\} \lambda_{i+1} - \mu M_{i+1} \\ &= \left\{ \beta_{i+1} \left[ b_{i+1} \left( 1 - e^{-\frac{-s_{i+1} M_i}{b_{i+1}}} \right) \right] P \right. \\ &\quad \left. - z_{i+1} M_{i+1} \right\} \lambda_{i+1} - \mu M_{i+1} \end{aligned} \quad (6ii)$$

and

$$\frac{dP}{dt} = \phi_{i+1} q_{i+1} \left[ \frac{dM_{i+1}}{dt} \right].$$

Despite its more daunting appearance, one can see that  $f(\cdot)$  and  $g(\cdot)$  are per capita forms of the G-B model, where  $M_i$  is the mass of  $N$  and  $M_{i+1}$  is the mass of  $P$ ,  $b_i$  and  $b_{i+1}$  are functions of within-trophic-level mass, the parameters correct the mass acquired for the costs of within-trophic-level acquisition and assimilation, and the time-varying supply-demand ratio  $\phi_i$  and  $\phi_{i+1}$  correct the constants  $q_i$  and  $q_{i+1}$  in the number dynamics models for the effects of resource acquisition shortfalls. Shortfalls cause the average size of prey and predator to vary (Gutierrez et al. 1981), and there are many ramifications of this. However, before proceeding to the development of age-structure models, the relationship of Eq. 6 to the logistic model is outlined.

*Relationship to the logistic model*

In the absence of predation and under constant conditions, the parameters  $\lambda_i$ ,  $\beta_i$ , and  $z_i$  in Eq. 6i are constants, and the task is to show that model simplifies to the logistic model. Specifically, if we assume that the

resource base  $M_{i-1}$  is constant ( $K$ )

$$\frac{dM_i}{dt} = \left\{ \beta_i \left[ b_i \left( 1 - e^{-\frac{-s K}{b_i}} \right) \right] N - z_i M_i \right\} \lambda_i. \quad (7)$$

Because  $\phi$  is a function, we cannot substitute  $\phi_i q_i M_i$  for  $N$  to make Eq. 7 totally dependent on  $M_i$ . Multiplying and aggregating the constants in Eq. 7 yields

$$\frac{dM_i}{dt} = r \left( 1 - e^{-\frac{-s K}{b_i}} \right) N - e M_i. \quad (7i)$$

If we redefine part of our model, it simplifies to

$$\frac{dM_i}{dt} = r \hat{f}(\cdot) N - e M_i. \quad (7ii)$$

As in the logistic model equilibria occur when  $\frac{dM_i}{dt}$  equals 0, and in Eq. 7ii this occurs at  $M_i = 0$  and when  $e M_i$  equals  $r \hat{f}(\cdot) N$ . In the extreme case  $\frac{dM_i}{dt}$  may be negative. The terms  $r \hat{f}(\cdot) N$  and  $e M_i$  are in units of  $M_i$  and may be viewed as resources acquired and respiration costs, respectively. A plot of  $\frac{dM_i}{dt}$  on  $M$  yields a left-biased parabolic function characteristic of logistic population growth. The number dynamics have the same properties because of the definition of  $dN/dt$  in Eq. 6i. Similar logistic effects of feeding rates on population growth were proposed in a theoretical model by Rapport and Turner (1975).

RELEVANCE OF PHYSIOLOGICALLY BASED  
RATIO-DEPENDENT MODELS TO THE  
DYNAMICS OF REAL AGE-STRUCTURED  
POPULATIONS

Correcting the linkage between mass and number using the supply-demand ratio ( $\phi$ ) resolves some of the problems of time-varying changes in population quality (Eqs. 6), but to evaluate these effects in the field requires that age structure and the effects of age-specific resource demand, acquisition, and allocation be introduced to the dynamics described by Eqs. 6. To help bridge this vexing gap, an age-structure model utilizing the metabolic pool paradigm described above is used to model a supposedly simple system, A. J. Nicholson's (1954a, b) classic laboratory study of sheep blow fly (*Lucilia cuprina* Weidman) dynamics. This is done as a prelude to discussing tri-trophic applications to nature.

*An age-structure model of  
Nicholson's blow flies*

Some age-structure models that may be used to describe the dynamics of linked mass and number in age-structured populations are the well-known Leslie (1945,



1948) and von Foerster (1959) models, a similar model with multiple attributes proposed by Sinko and Streifer (1967), and the distributed delay models (Manetsch 1976, Vansickle 1977, Nisbet and Gurney 1984, Gutierrez et al. 1984, Severini et al. 1990). These models have obvious common mathematical origins (Plant and Wilson 1986), but such models including realistic biology seldom have analytical solutions and must be evaluated numerically (Wang et al. 1977).

Here a distributed maturation time population model is used as the population dynamics shell. In the absence of attrition, the maturation times of members of a cohort initiated at the same time have a characteristic average and variance. The theoretical basis for this model was outlined by Severini et al. (1990). In the models, demands and allocations for growth and reproduction are age-specific.

*Nicholson's experiments.*—Blow fly larvae were fed sheep liver and the adults were fed liver and sugar water. In some studies, the larvae received a constant, usually inadequate daily supply of liver and the adults were given food ad lib. In other studies adult food was restricted, and the larvae were fed an excess. The adult feeding experiments were not modeled because it required additional assumptions about the need for adults to feed before producing eggs, their consumption rates, and the adult parameters  $\beta$ ,  $z$ , and  $\lambda$ . Only the 50 g of liver experiment is reported here, but equally good results were achieved for the 25-g experiment using the same model (see Gutierrez 1992). For consistency of units, the liver provided as food was converted to dry biomass assuming a 70% water content.

*Parameters of the model.*—The data to estimate the theoretical parameters of the metabolic pool model used to estimate the function  $b$  are not found in Nicholson's reports and the following reasonable estimates were made: dry mass of an egg is 0.1 mg; maximum fecundity is 10 eggs·female<sup>-1</sup>·d<sup>-1</sup> (Readshaw and Cuff 1980); maximum larval dry mass is 50 mg ( $M_{\max}$ ); the maximum daily age-specific assimilation rate was estimated from a simple exponential function on age fit between the initial mass (0.1 mg) and the maximum mass just before pupation (50 mg); the combined respiration ( $z$ ) and conversion ( $\lambda$ ) rate for liver ingested by larva is 0.3 mg·mg<sup>-1</sup>·d<sup>-1</sup>; the proportion egested ( $1 - \beta$ ) is 0.1. The average developmental times of the egg, larval, pupal, pre-oviposition, and mature adult periods are 2, 6, 5, 2, and 6 d, respectively, for a total of 21 d (Nicholson 1954a, b). These values were used to estimate  $b$  in the G-B model (see Gutierrez et al. 1988). For convenience the number of age classes in the distributed delay dynamics model was set equal to the average longevity.

Nicholson observed that fly survivorship and fecundity varied with size, which reflects the nutritional his-

tory (i.e., food supply/demand) of the individuals (Nicholson 1955). Baumgaertner et al. (1981) showed that survivorship in several insects under laboratory conditions was affected only at low levels of food despite large reductions in size. Specifically, Nicholson observed that small larvae produced under severe competition for food failed to pupate successfully. In the model 10 mg is assumed to be the threshold size for pupation (i.e., a generation level supply-demand ratio  $\hat{\phi} = 0.2$ ).

Fecundity in the Australian bush fly, for example, is known to vary with size (e.g., Tyndale-Briscoe and Hughes 1969), and in the blow fly model maximum fecundity was scaled by the ratio ( $0 < \frac{M(t,a) - 10 \text{ mg}}{M_{\max} - 10 \text{ mg}} < 1$ ), where  $M(t,a)$  is the average mass of adults of age  $a$  at time  $t$  and 10 mg is the smallest possible size.

Lastly, it is safe to say that the fly larvae were not always fed at the same time each day, the water content and nutritional value of the liver were not constant, and other experimental mishaps no doubt occurred. Since the food supply was nearly always limiting for the larvae, variations from a standard would be akin to providing variable rates of food. This variability was introduced in the model via a linear probability function that scaled the daily food supply. This function had an expected mean of 1 and a range of 0.5 to 1.5.

*Simulation of blow fly dynamics.*—The model was started using 100 new adults, a 1:1 sex ratio was assumed, the model was run for 500 d, and as in Nicholson's reports, only the data for days 240–440 are shown (Fig. 3).

Reasonable fits to the data, including the double humps that worried Gurney et al. (1980), were obtained. Although better fits were obtained here than those reported by prior workers (May 1973, Oster and Takahashi 1974, Gurney et al. 1980, 1981, Readshaw and Cuff 1980), this is considered a trivial point. As expected, the amplitude of the peaks was irregular due to stochastic food, but the period of the population cycles did not change compared to runs where the stochasticity was absent. Variations in food supply are seen as the irregular pattern in the supply–demand ratio (Fig. 3b) and explains much of the underlying dynamics. The ratio decreased when larval numbers increased indicating competition for food, low mature larval size (Fig. 3c), and in the extreme, poor pupation success. The latter is seen as the sharp troughs in the pupal peaks (Fig. 3d and in Nicholson's data). More important, one sees striking similarities between some of the observed (O) and simulated (S) peaks: O(1) and S(3); O(2) and S(5); O(3) and S(4); O(5) and less well O(6) and S(1). Similar peaks are compared in Fig. 4, suggesting that variability in the rate of food supplied and

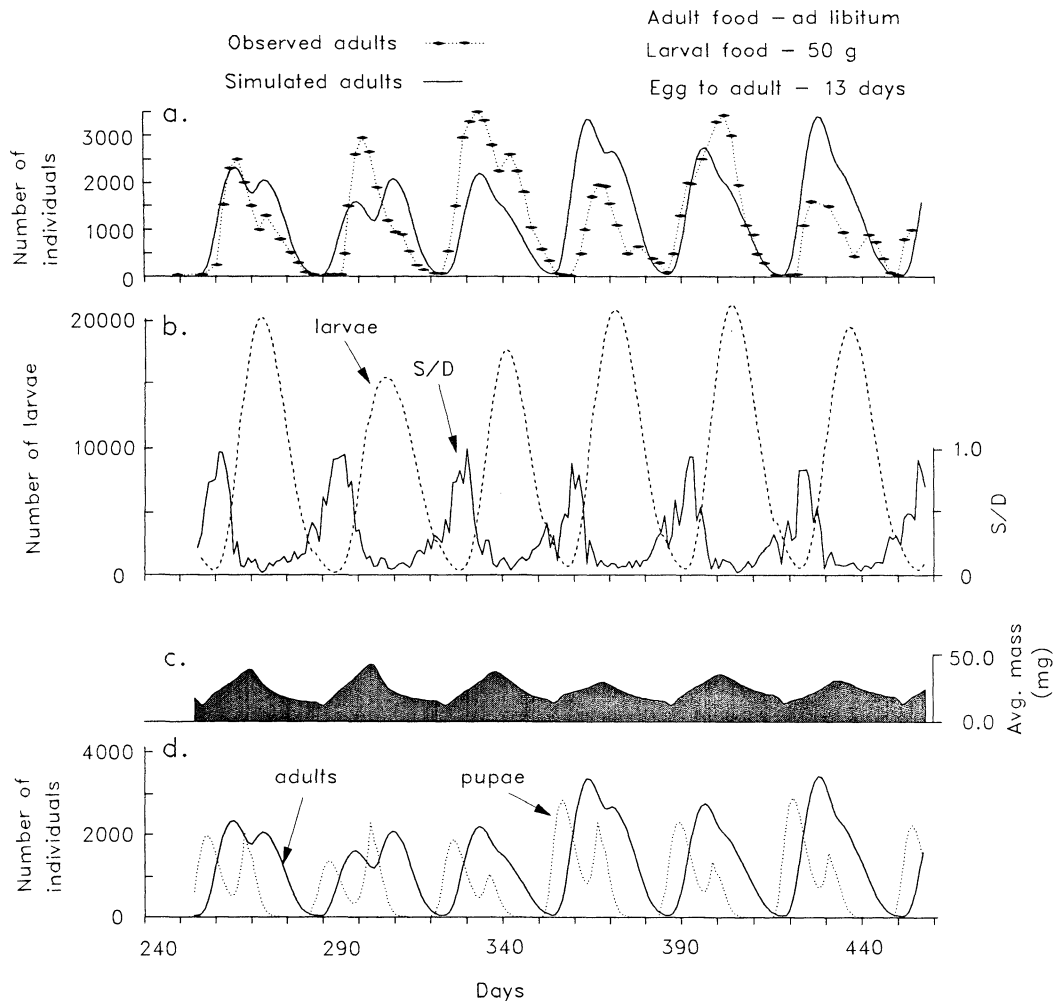


FIG. 3. Stochastic simulation of Nicholson's blow fly data for the 50 g larval food and ad libitum adult food treatment using the metabolic pool approach for the acquisition and allocation functions and the distributed maturation time model to simulate the population dynamics: (a) observed and simulated data, (b) simulated larval population and the resulting supply demand ratio ( $S/D$ ), (c) average adult mass, and (d) simulated adult and pupal numbers to illustrate the origins of the adult double peaks.

its effects on size and hence resource demands and resultant fecundity and pupal survival are sufficient to explain the observed adult dynamics.

The advantage of this model over prior attempts to model these data is that the dynamics emerged by considering the processes of resource demand, acquisition, and allocation as they affect age-specific growth, reproduction, and survival, no explicit time delays which automatically led to the oscillations were included, and the data are independent of the model. Embedding the dynamics of assimilation costs (i.e., the metabolic pool) adds the realism required to model field populations, especially when some of the parameters of the model are functions of environmental variables (e.g., solar

radiation, rainfall, temperature, etc.; see Gutierrez et al. 1988).

#### EXTENSION OF THE PARADIGM TO MULTI-TROPHIC FIELD POPULATIONS

Extension of this paradigm in an age structure setting to tri-trophic interactions that compare model predictions to field data has occurred in diverse systems such as alfalfa, apple, cassava, cotton, grape, and rice (e.g., Gutierrez and Wang 1976, Wang et al. 1977, Gutierrez et al. 1984, 1988, 1990, Graf et al. 1990, Wermelinger et al. 1991, Gutierrez 1992, etc.). The perceived complexity of the models has obscured their theoretical foundations and as such their origins have not been

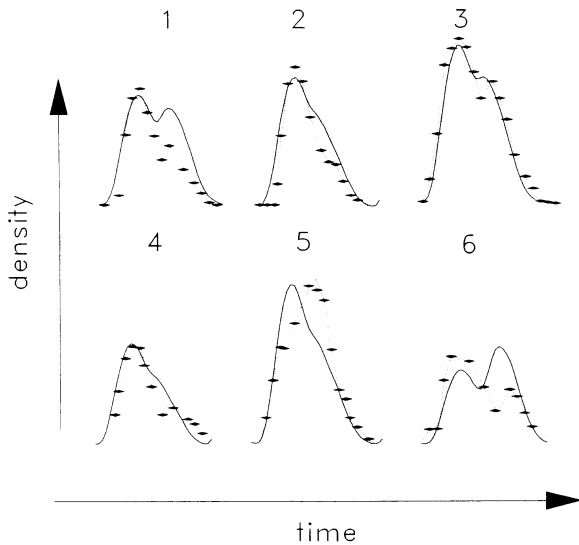


FIG. 4. Comparisons of segments of observed and predicted blow fly dynamics. Meaning of — and ···· as in Fig. 3.

generally understood. Here the paradigm is applied to modeling the dynamics of two species of *Acyrtosiphon* aphids in an alfalfa ecosystem.

#### *An alfalfa ecosystem* (Gutierrez et al. 1984, 1990)

More than 1500 species of arthropods are found in the alfalfa (*Medicago sativa* L [symbol A in the diagram in Fig. 5]) ecosystem in California (Neuenschwander, Hagen, and Smith 1975), but most are thought not to strongly interact (Gilbert et al. 1976) and/or their tenures in alfalfa are short and unobtrusive. All of these species including alfalfa are exotic, with the Egyptian alfalfa weevil (*Hypera brunneipennis* Boh. [W]) being the most serious pest. In California's mediterranean climate of wet (November–April) and dry (May–October) seasons, the blue alfalfa aphid (*Acyrtosiphon kondoi* Shinji [B]) and pea aphid (*A. pisum* Harris [P]) reproduce asexually throughout the year. The spotted alfalfa aphid (*Therioaphis trifolii* f. *maculata* Buckton) is currently not an important component of the system, and is thought to have been controlled by host plant resistance and introduced parasitoids. The fungal pathogen *Pandora neoaphidis* (R & H) Humber [F] attacks pea aphid at a rate 10 times that of the blue aphid (Pickering and Gutierrez 1991), and the aphidiid parasitoid *Aphidius smithi* Sharma and Subba Rao is host specific to pea aphid. Another parasitoid, *A. ervi* Haliday, attacks both aphids, but it was not present in the 1977–1978 study. *A. ervi* has since become the dominant species, but its impact is not evaluated here. A complex of lady beetles (*Hippodamia convergens*

Guerin, *H. qinqisignata ambigua* LeConte, *Coccinella californica* Mann., and *C. novemnotata franciscana* Mulsant) are predacious on these aphids, and they are included here in generic form. Only the salient points of the systems model are reviewed here (see Gutierrez et al. 1990).

The interactions in this system are complicated, but using the same metabolic pool ratio-dependent supply-demand paradigm and the same linked mass and number age-structured population dynamics model for each species greatly simplifies the problem (Gutierrez et al. 1987). All of the species are poikilothermic; hence the maximum assimilation rate  $A$  and the parameters  $z$  and  $s$ , and hence the function  $b$  of the metabolic pool models will vary with temperature at rates characteristic for each species (Fig. 5a; Gutierrez et al. 1981). The Frazer and Gilbert model was used for parasitoids, and the predator form (i.e., G-B) is used for photosynthesis in plants (i.e., they are light predators) and for predation by herbivores and true predators (see Gutierrez et al. 1981, 1988). In the model, time and age are functions of temperature and time (i.e., physiological time) (see Gilbert et al. 1976). Developing the model based mostly on laboratory data makes the models independent of the field data, which were collected at Fresno, California during 1977–1978 (Gutierrez et al. 1984).

Constructing the model in a modular fashion enables one to evaluate the dynamics of the species interactions from many perspectives by simply adding or deleting species. Here the exercise is limited to examining the role of the pathogen *P. neoaphidis* and the parasitoid *A. smithi* in determining species composition and dynamics of *Acyrtosiphon* aphids (see Gutierrez et al. 1990). The model runs in approximately 1 min on an IBM 386 microcomputer with a math co-processor.

*Simulation of the system.* — In the absence of natural enemies the observed and simulated aphid populations explode to very high levels (Gutierrez et al. 1990). However, when all interacting species in the system are included (Fig. 5b), the model reproduces the field data for blue aphid rather well, but the predicted August–September peak of pea aphid is greatly damped, and as observed the aphid numbers are low during spring of 1977 and January–February of 1978. When the fungal pathogen is removed, the dynamics of the blue alfalfa aphid are little affected, pea aphid are higher in spring 1977 and January–February of 1978 than observed, and the summer peak is still much too low (Fig. 5c). However, removing the aphidiid parasitoid and reintroducing the pathogen produces the right dynamics for aphids (Fig. 5d) throughout the entire period.

The model suggests that the pathogen enables blue alfalfa aphid to coexist at high levels with pea aphid and that the current rarity of *A. smithi* is due to the



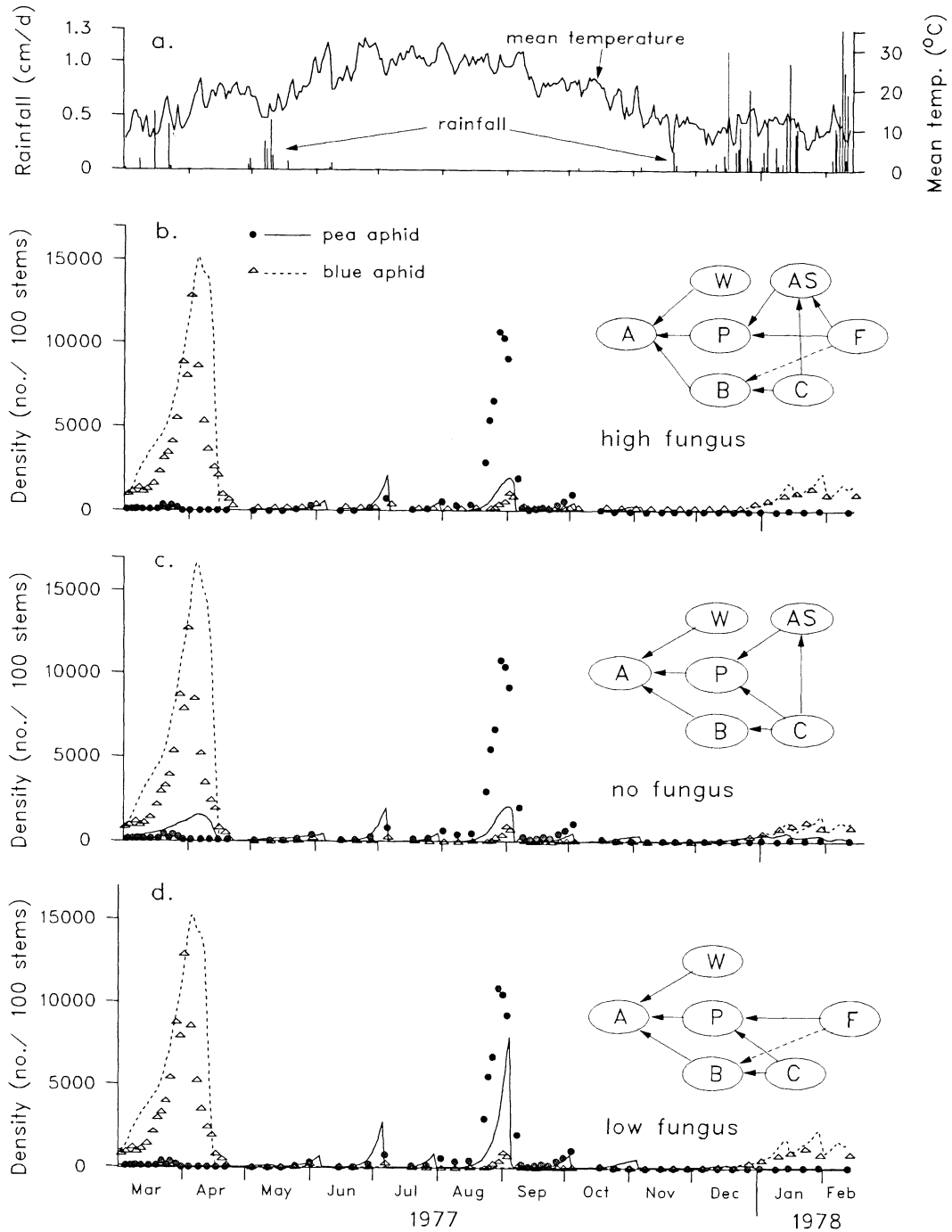


FIG. 5. Simulated and observed data on dynamics of pea (P) and blue (B) alfalfa aphids in an alfalfa (A) agroecosystem interacting with Egyptian alfalfa weevil (W), an aphid fungal pathogen (F), aphidophagous lady beetle predators (C), and the pea aphid specific parasitoid (AS): (a) rainfall and average temperatures are indicated but solar radiation and irrigation are part of the weather file; (b) all interacting species; (c) the same as system (b) minus the pathogen; and (d) the system (b) minus the parasitoid. Only the dynamics of the aphids are indicated, and the arrows in the icons indicate the trophic relationships (dashed lines indicate weak relationships).

severe suppression of its obligate pea aphid host by competition from blue aphid and more important mortality from the pathogen *Pandora* during rainy periods. Coccinellid predation affects both aphids and the immature stages of the parasitoid in a frequency-dependent manner and cannot cause preferential displacement. The current 5-yr drought in California has seen a resurgence of pea aphid, but not its parasitoid *A. smithi*, leading one to suspect that it has been permanently displaced in the alfalfa ecosystem by the selective fungal mortality. The model predicts that fungal mortality should be less important and coccinellids more important during periods of drought, and this is what is observed.

#### A HISTORICAL PERSPECTIVE

Many of the ideas that are the basis of this paper are not new. Among them are the notion that the success of organisms in obtaining resources (e.g., food) is a major determinant of their birth and death rates, and in the aggregate the population rate of increase. However, most prior models sought to understand life history strategies and not to model specific systems. For example, Gatto et al. (1989) review much of the theoretical literature and propose an optimization model based on the organism basic physiology to predict age-independent fertility and mortality rates as a function of food availability. In contrast, Gutierrez and Wang (1976) sought to model natural systems, and proposed that demand-driven (albeit ratio-dependent) models provide better descriptions of the resource acquisition process than do purely search-driven models because: (1) they have a physiological basis, (2) the prey acquisition rate is limited to a realistic range (see also Mills 1981), (3) the time-varying ratio of resource acquired to that demanded ( $\phi$ ) is a natural consequence, and (4) as demonstrated for blow fly,  $\phi$  provides an appropriate method for regulating birth, growth, and death rates at the per capita and population levels (Gutierrez and Wang 1976, Gutierrez et al. 1981, 1987, 1988).

The notions of the metabolic pool are also found in prior models. For example, Readshaw and Cuff (1980) derived functions for predicting birth and egg-to-adult survivorship rates for sheep blow fly based on the initial amount of liver per egg (i.e., ratio dependence) (Fig. 6a, b). The data were average values from several of Nicholson's experiments, and the resultant functions may be easily interpreted using the metabolic pool model (Eq. 4i, Fig. 1; Gutierrez et al. 1981). For example, the constant 0.50 in Fig. 6a is the sum of respiration and tissue conversion costs in terms of eggs per adult per day; the metabolic compensation point is 0.14 mg of liver per adult per day estimated by solving for  $e(t)$  equal to zero, and 3.59 eggs are produced per milligram of liver per adult per day above

the compensation point. Egg-to-adult survivorship (Fig. 6b) may be interpreted as the ratio of the initial per-capita supply of liver per egg to the per-capita demand to produce a mature adult of maximum size (i.e.,  $\phi$  = mass obtained/mass demanded) (Gutierrez et al. 1981). The shape of the survivorship function emerges by noting that the mass of liver acquired per larva is expected to be concave with respect to mass of liver offered per larva (i.e., Nicholson's competition curve and ratio dependence), but the demand is expected to be reasonably constant under constant conditions. The ratio yields a normalized concave survivorship function similar to that proposed from first principles by Gutierrez et al. (1981, 1984). Similar functions are common in the literature (Beddington et al. 1976). The relationship to the ratio-dependent approach is also seen by observing that the  $x$  intercept in Arditi et al.: Fig. 2 (1992) is the metabolic compensation point for *Daphnia*. The effects of variable conditions are accommodated with equal ease.

*Nicholson and the metabolic pool model.*—Nicholson (1954a), unwittingly I suppose, proposed the rudiments of a metabolic pool model in his equation for equilibrium density of adults ( $N_E$ ):

$$N_E = \frac{g(1 - \lambda - w)}{q} \quad (8)$$

In this model  $g$  is the rate of generation of the governing resource (i.e., mass of liver),  $\lambda$  is the fraction of this lost to the animals due to other "agencies" (i.e., all costs),  $w$  is the fraction wasted as the animals scramble for food (i.e., that eaten by individuals that failed to produce adults), and  $q$  is the minimum per-capita quantity of liver required for an egg to develop to maturity.

In the metabolic pool paradigm under constant conditions,  $\lambda$  would include respiration, egestion, and conversion costs,  $w$  remains as defined, but  $q$  must be the maximum genetic per-capita demand for liver from egg to pupa (i.e.,  $b$  in Eq. 4), and  $\hat{N}$  would be the number of the largest sized individuals that could be produced from the resource  $g$ . Defining  $q$  in this way and dividing both sides of Eq. 8 by the initial number of eggs in the cohort ( $N_e$ ) that feeds on  $g$  yields the supply-demand ratio ( $\phi$ ).

$$0 < \phi = \frac{\hat{N}}{N_e} = \frac{g(1 - \lambda - w)}{qN_e} \leq 1. \quad (9)$$

Larvae obtaining insufficient food to pupate die, suggesting a food supply-demand threshold for survival (i.e.,  $\phi$ ) and causing the wastage rate  $wg$ . In my model, a survivorship function (Eq. 10) was applied at the beginning of the pupal stage.

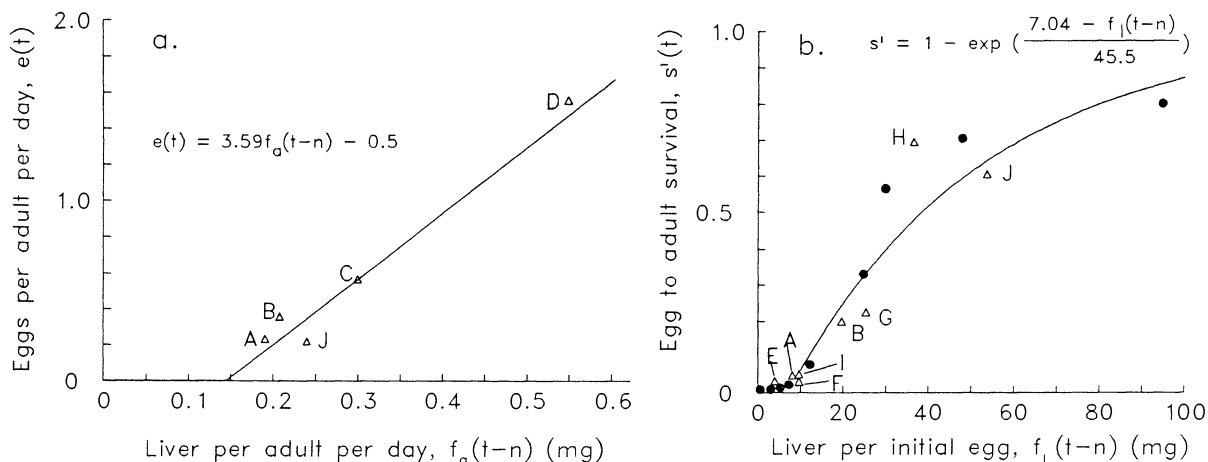


FIG. 6. Fecundity (a) and survivorship (b) in sheep blow fly as functions of the per capita supply of liver. The functions were estimated from several (i.e., the upper case letters A–J) of A. J. Nicholson's laboratory experiments (redrawn from Readshaw and Cuff 1980).

$$\text{survivorship} = \begin{cases} 1 & \text{if } M > \hat{\phi}q \\ 0 & \text{if } M \leq \hat{\phi}q \end{cases} \quad (10)$$

The threshold  $\hat{\phi} = 0.2$  proved critical to modeling Nicholson's data.

#### CONCLUSIONS

Ratio-dependent theory indicates the nature of the problem, and for some systems may provide sufficient detail. However, incorporating the physiology of resource demand and allocation in an appropriate functional response model enables us to model simple (laboratory blow fly populations) or complicated tri-trophic systems with reasonable understanding and accuracy. In the model the biology of assimilate demand drives the ratio-dependent functional response model determining the per-capita resources acquired, and the ratio of supply to demand is used to control all aspects of growth, reproduction, and survivorship (and emigration) in the dynamics model. Ratio-dependent models lacking this physiology are simply rougher approximations of the biology of resource acquisition and allocation, and their consequences to population birth and death rates.

#### ACKNOWLEDGMENTS

Special thanks are due N. J. Mills for his interest and helpful suggestions, to Alan Berryman and Pamela Matson for the invitation to prepare this paper, to C. K. Ellis for his abundant technical help, and to an anonymous reviewer whose suggestions helped clarify some important issues.

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