MODELING THE AGE-SPECIFIC PER CAPITA GROWTH AND REPRODUCTION OF *RHIZOBIUS LOPHANTHAE* (*COL.: COCCINELLIDAE*)

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A per capita model for the growth, development and reproduction of the coccinellid predator *Rhizobius lophanthae* (Blaisd) feeding on the oleander scale (*Aspidiotus nerii* Bouche (Homoptera: Diaspididae)) was developed. A thermal threshold for development of 9.4°C was found. Under conditions of unlimited food, the relationship of mass at time t + 1 to that at t (in days at 25°C) suggests an 8.7 percent growth rate per mg larvae per day at 25°C. An adult female beetle produces approximately 20 eggs per day while consuming an average of 8.5 scales/day. This is approximately 2.16 eggs per scale consumed above the maintenance level of 1.88 scales per day. More precisely, this compensation point is 0.12 mg of prey/mg of predator/day at 25°C and the egestion rate is $1 - \beta = 0.63$.

KEY-WORDS: *Rhizobius lophanthae*, energy flow, metabolic pool model, oleander scale.

The Australian coccinellid *Rhizobius lophanthae* (Blaisd) has been introduced into several countries for the control of armored scales (Diaspididae) and has proved useful in a variety of crops (Greathead, 1973). In Northern California, the oleander scale *Aspidiotus nerii* Bouche (Homoptera: Diaspididae) is common on bay tree (*Umbellularia californica* (Hopk. and Arn.) Nut.) and it is attacked by the parasitoid *Aphytis chilensis* Howard (Hymenoptera: Aphelinidae) and the predator *R. lophanthae*. Based on field evidence of attack rates (*i.e.*, the characteristic bites vs. parasitoid emergence holes), this coccinellid was found to be the most important mortality factor of *A. nerii* on bay tree (Pizzamiglio, 1985). However, despite its importance, the biology of *R. lophanthae* has not been characterized and no attempt has been made to build a model to simulate its dynamics in the field. As a precursor to this development, a metabolic pool model of the per capita growth, reproduction and development of *R. lophanthae* was formulated based on laboratory studies of prey consumption and assimilation (Gutierrez *et al.*, 1981; Delucchi *et al.*, 1983). This model provides the basis for evaluating the role of this predator dynamics on this plant-herbivore-predator-parasitoid system (Gutierrez *et al.*, 1994).

MATERIAL AND METHODS

THE METABOLIC POOL MODEL

The metabolic pool model describing the rates of food acquisition and allocation proposed by Gutierrez *et al.* (1981) has been used extensively to model plant and animal growth and development. It is used here to model these processes in *R. lophanthae* (see fig. 1). The rate model (1i) summarizes these processes per day at 25°C. Note that a change in time is the same as a change in age ($\Delta a = \Delta t$).

$$\Delta W(a) = \Delta G(a) + \Delta R(a) = \left[g\left(\frac{\text{prey mass}}{\text{predator mass}} \right) \beta - z \right] \lambda W(a), \qquad (1i)$$

where $\Delta W(a)$ is the per capita rate of biomass assimilation by a female beetle of age a with components ΔR being the per capita assimilation rate to reproduction and ΔG the growth rate, $g(\,.\,)$ is the consumption rate of prey, β is the proportion of food not egested, z is basal per unit of mass respiration rate, W is predator biomass (mg) at age a, where $\lambda = 0.75$ is the assumed conversion efficiency of assimilated food to consumer (see Gutierrez *et al.*, 1981).

Multiplying (1i) through by λ to simplify we get new constants $\theta = \lambda\beta$ and $Z = \lambda z$

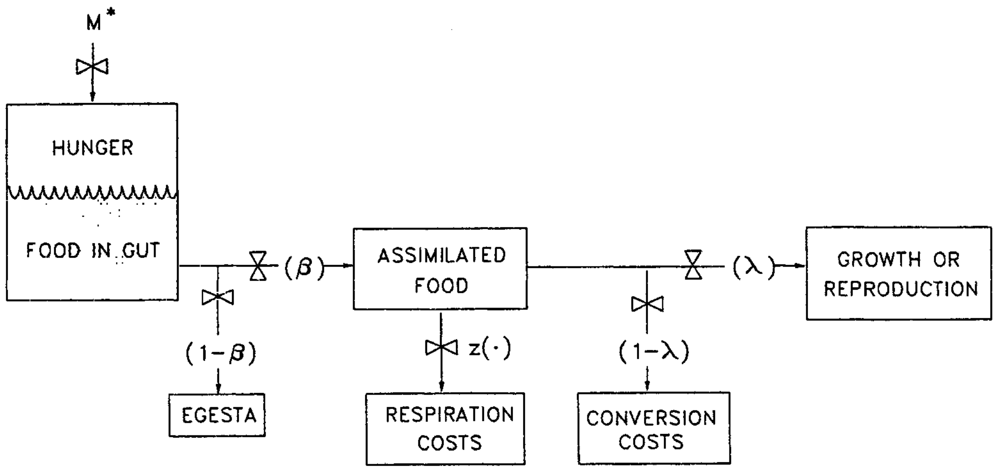

Fig. 1. Metabolic pool model for *Rhizobius lophanthae* (cf., Gutierrez *et al.*, 1981).

$$\Delta W(a) = \Delta G(a) + \Delta R(a) = (\theta g(\,.\,) - ZW(a)). \qquad (1ii)$$

where θ is food not egested corrected for conversion efficiency, and Z is the base respiration rate corrected for conversion efficiency. The goal of this study is to estimate the parameters for (1).

Insect colonies reared in the laboratory

Colonies of *A. nerii* were started from inoculum provided by Professor R. L. Luck (University of California, Riverside). *A. nerii* colonies were maintained continuously on citron melon (*Citrulus vulgaris citroides*) (Pizzamiglio, 1985), and even aged populations of scales used in the experiments were reared on buttercup squash (*Curcurbita* spp.). The colony of *R. lophanthae* was started from specimens collected and identified by Professor K. S. Hagen (University of California, Berkeley). All experiments, except those used to determine the lower developmental threshold temperature were conducted at 25°C and 16 h photophase.

LABORATORY STUDIES ON *ASPIDIOTUS NERII*

Five groups of 10 scales each in different stages of development were measured for body and carapace diameter using an ocular micrometer. The dry weights of scale body and carapace were measure on a Cahn C-33 microbalance after two weeks in a desiccator.

LABORATORY STUDIES ON *RHIZOBIUS LOPHANTHAE*

Developmental temperature thresholds — The lower temperature thresholds for the developmental of the egg-pupal and the pupal-adult stages of *R. lophanthae* were determined by observing, once a day, cohorts in incubators at 15, 20, 25 and 30°C and 16 h photophase. Humidity was not controlled in these studies but generally varied between 50-70%. Buttercup squashes heavily infested with even-aged oleander scales were exposed to oviposition/predation by *R. lophanthae* females for 24 h, and 30-40 of their progeny observed throughout their life cycle at each temperature regime. As the density of scales on a squash became small, the predators on it were transferred to another infested squash. Pupae were kept in Petri dishes under the same conditions as the larval stage until adult emergence.

Larval prey consumption and growth rates — Five groups of five predator larvae were reared from hatching until pupation on buttercup squash with unlimited even-aged scale. The weight of the predator larvae and the number of scales consumed were recorded daily. In this and in other studies, cadavers of attacked scales were marked with a permanent ink marker so that old attacks would not be confused with new ones.

Adult fecundity — Ten mated adults *R. lophanthae* females (5-6 days old), were isolated in small plastic containers on buttercup squash heavily infested with oleander scales. The number of scale consume and the number of eggs laid by the predator were recorded daily.

Respiration and egestion rates — Respiration rate (z, see (1)) at 25°C was estimated by starving fully fed adult females at room temperature and giving them only free water. The females were weighed daily to determine the rate of weight loss. The egestion rate $(1 - \beta)$ was approximated by substituting estimates of z, the mass of *A. nerii* consumed, and the mass of eggs produced in equation (1i).

RESULTS AND DISCUSSION

LABORATORY STUDIES ON *ASPIDIOTUS NERII*

Considering scales in different stages of development, figure 2a,b show a linear relationship between the dry mass of the *A. nerii* scale body and carapace to their respective diameters. The average body and carapace weights (W) of adult scales fed to *R. lophanthae* were 0.055 mg and 0.028 mg respectively, and the average diameters were 1.03 mm and 1.87 mm respectively. These values are very close to those estimated by Pizzamiglio (1985).

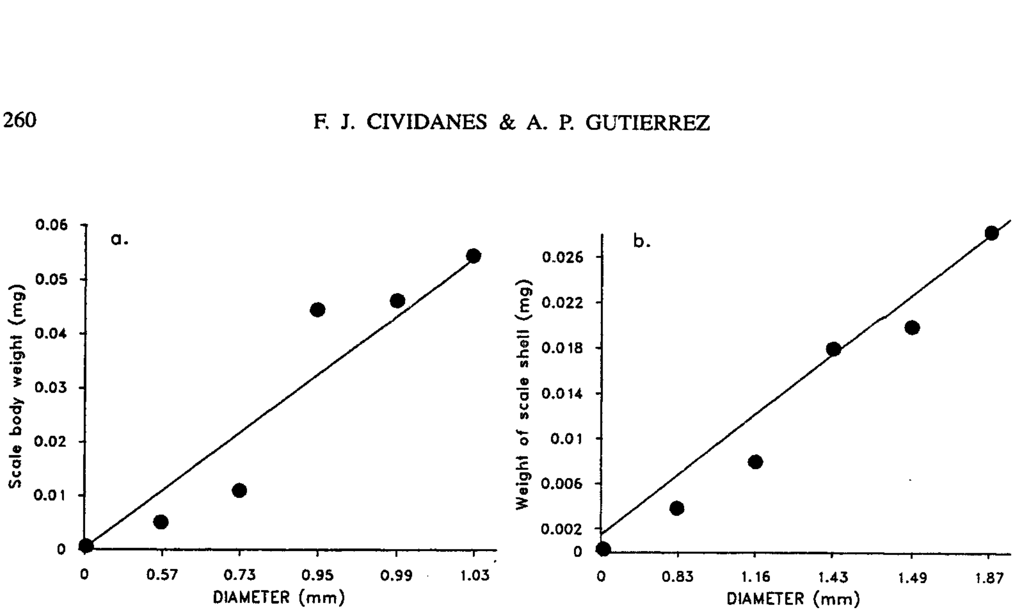

Figure 2. The relationship between *Aspidiotus nerii* dry weight and scale shell diameter: (a) scale body weight and scale shell diameter ($W_b = -0.0640 + 0.1129\,d$, $r^2 = 0.96$) and (b) scale carapace and scale carapace diameter ($W_c = -0.0175 + 0.0244\,d$, $r^2 = 0.99$).

LABORATORY STUDIES ON *RHIZOBIUS LOPHANTHAE*

Developmental temperature thresholds

The rates of development of egg to pupa and pupa to adult stage are linearly related to temperature in the range of 15-30°C (fig. 3), and the lower temperature threshold (τ) for development are 8.5°C and 10.3°C respectively, and the average threshold 9.4°C. This threshold is lower than the 11.6°C threshold found for the coccinellid *Propylaea 14-punctata* L. and 12.4°C for *Coccinella 7-punctata* L. (Baumgärtner *et al.,* 1987). In the present study, 15.6D° (= day degrees) accrued per day.

Larval growth rate

The wet larval weight (W) is an increasing function of age (fig. 4a) and can be estimated from egg hatch to pupation at 25°C by

$$W(a) = (0.0259\, e^{0.548\,a}), \quad r^2 = 0.98, \quad n = 8, \tag{2}$$

where 0.548 is a constant, a is age in days and the estimated average egg wet weight is 0.0259 mg. The parameters were estimated by regressing $\mathrm{Log}_e W(a)$ on age (a). The derivative of (2) yield the age specific growth rate. A rougher estimate may be obtained by plotting larvae weight at time ($W_a + 1$) on W_a yielding an average growth rate of 1.087 mg/mg/day (fig. 4b, $W_{a+1} = 0.31 + 1.087\,W_a$, $r^2 = 0.97$, $n = 100$). The constant converting wet weight to dry weight is 0.3023.

Larval consumption of prey associated

The relation between the cumulative number of prey consumed (Na) and the associated change predator larval wet weight (W) is

$$Na = -0.47 + 37.30\,W, \quad (r^2 = 0.99, n = 8) \tag{3}$$

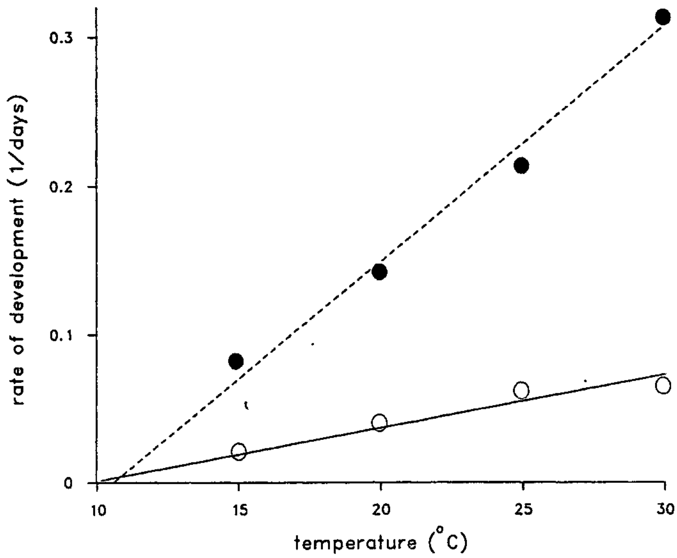

Fig. 3. The rate of development of *Rhizobius lophanthae* egg-larval stages (———, r = − 0.0282 + 0.0033 T, r^2 = 0.93) and the pupal stage (- - - -, r = − 0.1588 + 0.0154 T, r^2 = 0.99) on temperature T.

This means that 37.77 scale are consumed to produce a mg wet weight of predator larva. The dry mass of prey eaten per mg dry mass of beetle can be computed by multiplying Na by the average dry mass of a scale (0.055 mg) and correcting beetle wet mass to dry mass by multiplying by the constant 0.30. We find that 6.83 mg dry weight of scale are consumed to produce one mg dry weight of predator larva for conversion efficiency of 0.14. On a per day basis at 25°C, the dry mass of scale eaten per day (ΔS) is related to the change in predator dry weight per day (ΔW) as follows:

$$\Delta S = 0.10 + 6.07\,\Delta W, \quad n = 7, r - 0.98 \tag{4}$$

for an estimate of 6.17 mg dry weight of scale /mg dry weight of predator larvae /day (*i.e.*, on a dry weight basis 0.43 mg /mg/ D°). This value on a D° basis is higher than that calculated for the coccinellid *P. 14-punctata* (0.26 mg/mg/D° and *C. 7-punctata* (0.4 mg/mg/D°) (Baumgärtner *et al.*, 1987).

Adult consumption of prey

Adult predator females consumed on average 8.5 scales/day (fig. 4c) of average dry mass 0.055 mg for a total of 0.47 mg of scale/predator/day. If an average sized beetle is 0.83 mg dry weight, the consumption rate is 0.567 mg/mg/day (0.04 mg/mg/D°). This estimate is higher than for larvae. Furthermore, these values are difficult to compare with estimates from other studies in literature because the data were not reported in mass units. For

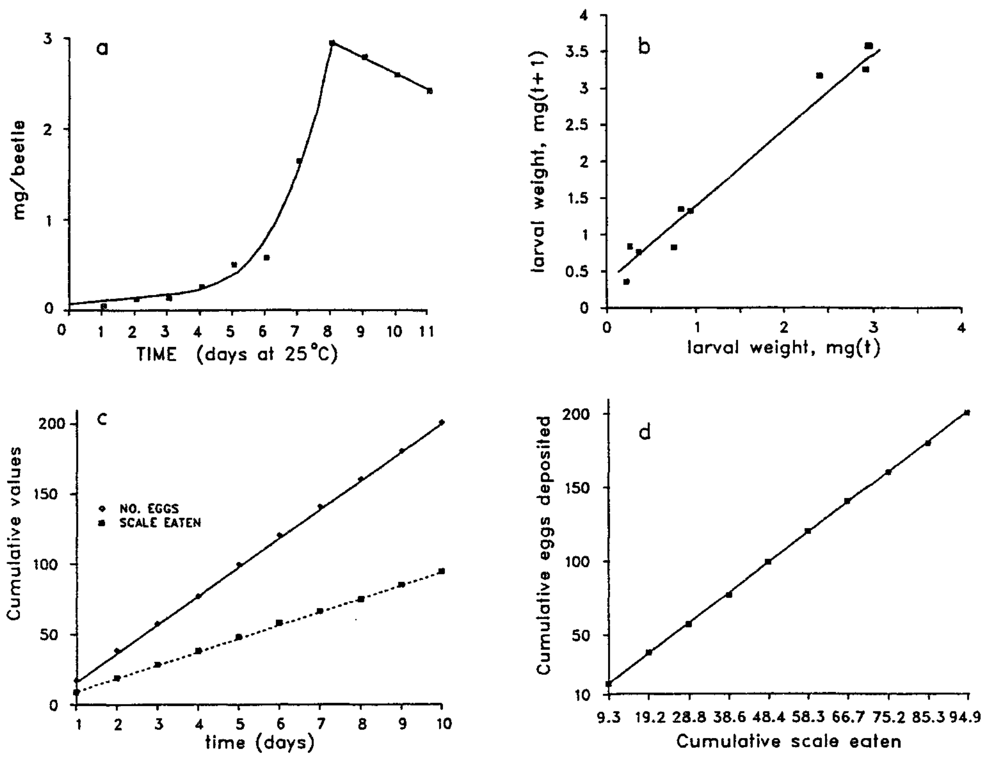

Fig. 4. The biology of *Rhizobius lophanthae:* (a.) the per capita wet mass plotted on age in days, (b.) the relationship of mass at time t + 1 to that at t (in days), (c.) the cumulative number of scales consumed and number of eggs produced on days, and (d.) the relationship of cumulative eggs deposited to cumulative scale eaten.

example, Marin (1983), using *Pinnaspis aspidistrae* (Sing.) (Homoptera: Diaspididae) as prey, found that *R. lophanthae* females consumed 12 scales/day while consumption by males is approximately a third that value.

Fecundity

From the 8.5 scales/day consumed per day, an *R. lophanthae* female deposits 20 eggs/day (fig. 4c). This is higher than the 16.5 eggs/day found for *Adalia bipunctata* L., kept at 22°C and feeding on *Myzus persicae* (Sulzer) (Inger-Johanne 1969). A linear relation (5) between eggs produced (E) and the number of oleander scales (S) consumed is seen in figure 4d.

$$E = -4.09 + 2.17\,S, \quad r^2 = 0.99, n = 10\,. \tag{5}$$

Respiration rates

For adults, the weight loss per starved beetle per day is shown in figure 5, and may be described by

$$W_{(a)} = W_0 e^{-ca} = 3.35 e^{-0.144a} \quad (6)$$

where $W_{(a)}$ is body mass at age a, W_0 is initial body weight of the beetles in this study (*i.e.*, 3.35 mg), $c = -0.144$ and a is days at 25°C. The constant c was estimated by regressing logW on a. Differentiating (6) and dividing by the average adult female /wet weight (3.35 mg) estimates the respiration rate mg/mg/day (*i.e.*, z at 25°C)

$$Z = dW/W(a)\,da = -0.482 e^{-0.14} / W(a) = 0.11 \text{ mg/mg/day}. \quad (7)$$

and $z = Z / X = 0.147$/mg/mg/day.

The base respiration rate z_0 can be estimated using the Q_{10} rule (8i) using measured values.

$$z\,(25\,°C) = z_0\, 2^{(25-\tau)/10} \quad (8i)$$

where the lower threshold for development is $\tau = 9.4$ °C. Solving (8i) for z_0 yields

$$z_0 = 0.05 \text{ mg/mg/day}. \quad (8ii)$$

The adult female maintenance respiration rate at 25°C may also be estimated from the oviposition experiments summarized by (5). At $E = 0$, S equals 1.88 scale/female/day yielding an estimate of $z = 1.88 \times 0.055/2.95/0.30 = 0.12$ mg/mg/day dry weight. Correcting for λ yields $Z = 0.15$ mg/mg/day.

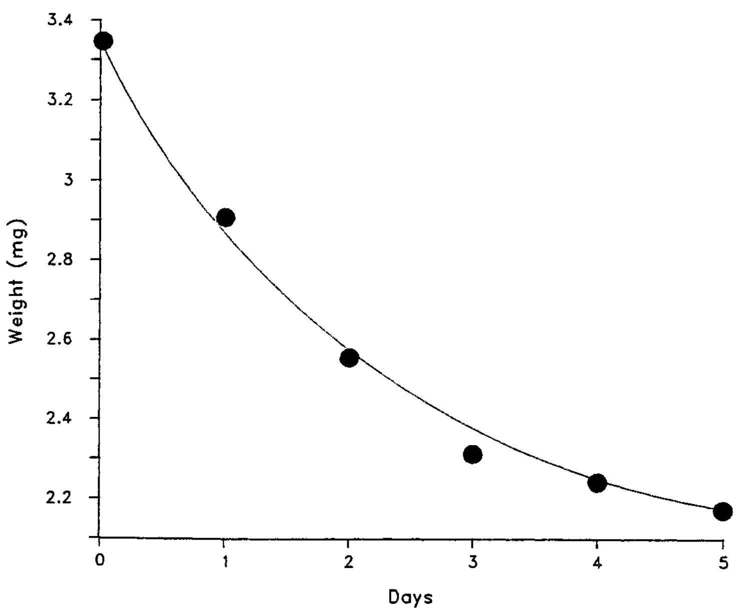

Fig. 5. The average weight of an adult female *Rhizobius lophanthae* on time starved.

EGESTION

The only unknown is the egestion rate $1 - \beta$, but this can be obtained by substituting the other known quantities in (1) and solving for β. For adults, this yields an egestion rate of $1 - \beta = 0.63$. The value of $\beta = 0.37$ for *R. lophanthae* is larger than that of *Hippodamia convergens* G-M ($\beta = 0.26$, Gutierrez *et al.*, 1981), but lower than for *P. 14-punctata* (0.68, Baumgärtner *et al.*, 1987) and *C. 7-punctata* (0.64, Baumgärtner *et al.*, 1987).

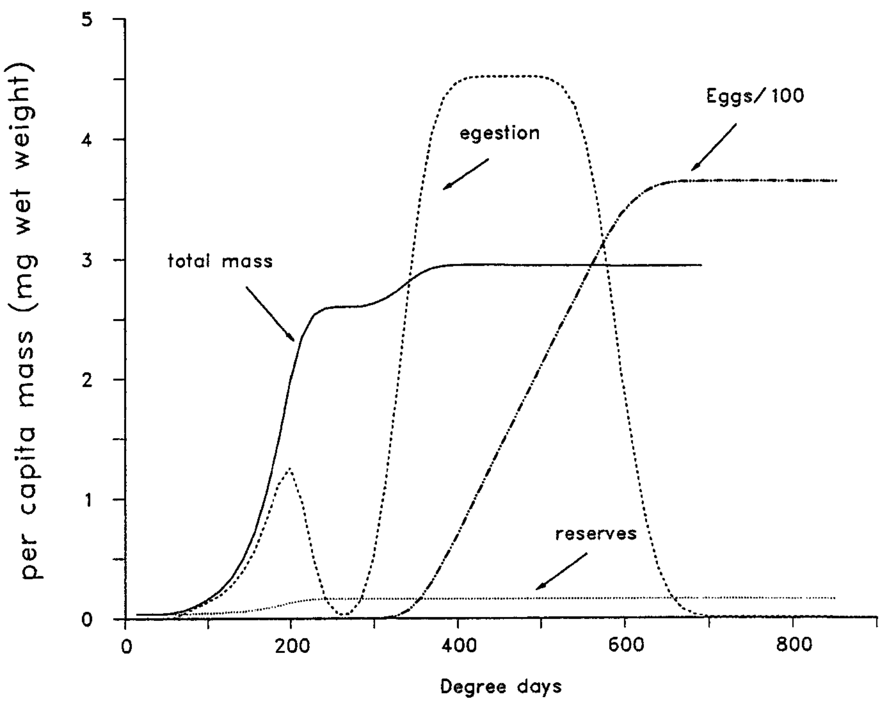

Fig. 6. Simulation of the growth and reproduction of the coccinellid beetle *Rhizobius lophanthae* with unlimited food.

A GENERAL MODEL FOR THE GROWTH AND REPRODUCTION OF *RHIZOBIUS LOPHANTHAE*

The coccinellid growth and reproduction are affected by the food consumption rate (see below) and environment temperature which alters respiration rate. According to model (1) assimilation can be modeled as

$$\Delta W(a) = \Delta G(a) + \Delta R(a) = [\beta g(\,.\,) - z]\,\lambda W(a)$$

$$= [0.37\,g(\,.\,) - 0.12]\;0.75\,W(a) \qquad (9)$$

However, for a general relationship, we define g (.) as a per unit mass functional response (Gutierrez *et al.,* 1981, 1984)

$$Na = W(a)\,g(\,.\,) = W(a)\,D\left[1 - \exp\left(\frac{\alpha m S}{DW(a)}\right)\right] \qquad (10)$$

where Na is dry mass of scale eaten, D is the maximum demand rate for prey (0.56 mg/mg/day), W is dry weight of a predator of age a, α is the proportion of prey that many be attacked (*i.e.,* the apparency rate of prey), and S is the number of scale of average dry mass m (= 0.055 mg). α may be estimated for a specific environment by observing beetle feeding responses at different levels of food and fitting (10) to the data (*e.g.,* DaSilva *et al.,* 1992).

The demand rate D (mg/mg/At) is viewed as the genetic potential for food consumption (g (opt.,.)) and assimilation to reach maximum size and fecundity (Gutierrez *et al.,* 1981). This value is the sum of all out flows from Figure 1, and is estimated by feeding experiments designed to estimate the various parameters (see above). From equations (1ii, 10), it is defined under optimal conditions as follows:

$$D = \text{maximum consumption rate} = g(\text{opt.},\,.\,) = (\Delta W_{(a)}/W_{(a)} + z)/\beta\,.$$

The predictions of this model are seen in figure 6 for non limited conditions, but other conditions including variable rates of food and temperature are easily accommodated (Gutierrez *et al.,* 1984, 1994). The reserves indicated in figure 6 can be estimated by starvation experiments where water is suplied. The initial weight and death weight provide a measure of how much reserves the beetle has.

RÉSUMÉ

Modèle âge-spécifique et par individu de croissance et reproduction de *Rhizobius lophantae* (Col.: Coccinellidae)

Un modèle par individu de la croissance, du développement et de la reproduction de *Rhizobius lophantae* Blais., coccinelle prédatrice de la cochenille du laurier rose (*Aspidiotus nerii* Bouché) (Hom.: Diaspididae) a été élaboré. Un seuil théorique de développement thermique de 9,4°C a été déterminé. Dans des conditions de nourriture non limitantes, la relation de la masse au temps t + 1 à la masse au temps t (en jours à 25°C) se traduit par un taux de croissance de 8,7% par mg de larve/jour à 25°C. Une femelle adulte du prédateur produit approximativement 20 œufs/jour alors qu'elle consomme une moyenne de 8,5 cochenilles/jour. Ceci représente 2,16 œufs par cochenille consommée en plus du niveau d'entretien de 1,88 cochenilles par jour. Plus précisément, ce point de compensation est de 0,12 mg/ mg de proie/ jour à 25°C et le taux d'excrétion est de $1 - \beta = 0{,}63$.

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