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GROWTH AND DEVELOPMENT OF IMMATURE LIFE STAGES OF *PROPYLAEA 14-PUNCTATA* L. AND *COCCINELLA 7-PUNCTATA* L. [*COL. : COCCINELLIDAE*] SIMULATED BY THE METABOLIC POOL MODEL

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The conversion of aphid prey tissue (*Acyrthosiphon pisum* Harris) into predator biomass (immature life stages of *Propylaea 14-punctata* L. and *Coccinella 7-punctata* L.) is calculated by plotting weight gain against assimilation (i.e. consumption minus egestion). This concept is added to the metabolic pool model by **Gutierrez** *et al.* (1981) that enables the simulation of growth and development of a predator on a physiological basis. Physiological time is expressed in daydegrees above lower development thresholds for both species. Visual examination of observed and calculated values showed that the model satisfactorily describes the growth patterns of the above predators.

KEY-WORDS : *Propylaea 14-punctata, Coccinella 7-punctata,* simulation model, growth, development, metabolic pool.

The pea aphid *Acyrthosiphon pisum* Harris is a pest in Swiss canning pea fields (**Meier**, 1955, 1981 ; **Suter & Keller**, 1977). **Suter** (1977) investigated its natural enemies and noted that the coccinellids *Propylaea 14-punctata* L. and *Coccinella 7-punctata* L. play an important role in reducing pea aphid populations. There is extensive documentation on the biology of *Coccinella 7-punctata* L. (**Hodek**, 1958 ; **Asgari**, 1966 ; **Blackman**, 1967a, b ; **Hodek**, 1973 ; **Hagen**, 1962, 1974 ; **Singhal**, 1976 ; **Obrycki & Tauber**, 1981) while little information is available on the bionomics of *Propylaea 14-punctata* L. (**Patrascanu**, 1964 ; **Sommer**, 1976 ; **Rogers** *et al.*, 1972). Also, no attempt has yet been made to build models to simulate the dynamics of the 2 coccinellids. With these models it would be possible to analyze the role of predators in the pea aphid life-system (**Delucchi** *et al.*, 1983). Recently new approaches have been proposed for explicative predation models which are based on the physiological mechanism of food acquisition and allocation. While **Nakamura** (1982) and **Sabelis** (1981), for example, built highly detailed models for specific predation processes, **Gutierrez & Baumgaertner** (1984b) attempted to use a general metabolic pool model, to study multitrophic interactions between populations of plants, plant parts, herbivores and their natural enemies. In this paper objectives and methods for modelling coccinellid predation are the same as those described by the above mentioned 2 authors, but an attempt is made to link the metabolic pool model with the aspects of the nutrition physiology. In this context the approach used by animal nutritionists (**Bickel**, 1977) has been followed and this is considered here much more important than the accurate estimation of certain parameters included in the models, as for instance respiration rate. The paper is, furthermore, restricted to growth and development of non-diapausing immature life stages under conditions of unlimited food, but indications are given how to make the model more general.

MATERIAL AND METHODS

THE METABOLIC POOL MODEL

Food ingestion, assimilation and allocation to metabolic processes are depicted in fig. 1, which is a modification of the model proposed by **Gutierrez** *et al.* (1981) and **Gutierrez & Baumgaertner** (1984a). In fig. 1 costs of converting prey into predator tissues are considered separately, as proposed by animal nutritionists (**Bickel**, 1977). Converted assimilates are allocated to meet respiratory costs in relation to body weight, temperature and predator activity. However, in this paper the respiratory costs are considered only as a function of the body weight under standard conditions (20°C, 70-90 % rh, 16/8 photoperiod). Once respiration costs are satisfied, converted assimilates are invested in larval growth, which includes the build-up of reserves. The model used here is a simplified version of fig. 1 and can be summarized for a time step of one daydegree as follows

$$\Delta W = c \cdot (1 - \beta) \cdot (1 - \delta) - \gamma(W) \quad [1]$$

where

W = body dry weight in mg
ΔW = change in body weight
c = consumption rate per mg predator
β = egestion ratio
δ = conversion ratio
γ = respiration rate per mg body weight for an inactive predator under standard conditions and unlimited food.

The physiological time is expressed here in daydegrees and various parameters of eqn. 1 are outlined in the following sections.

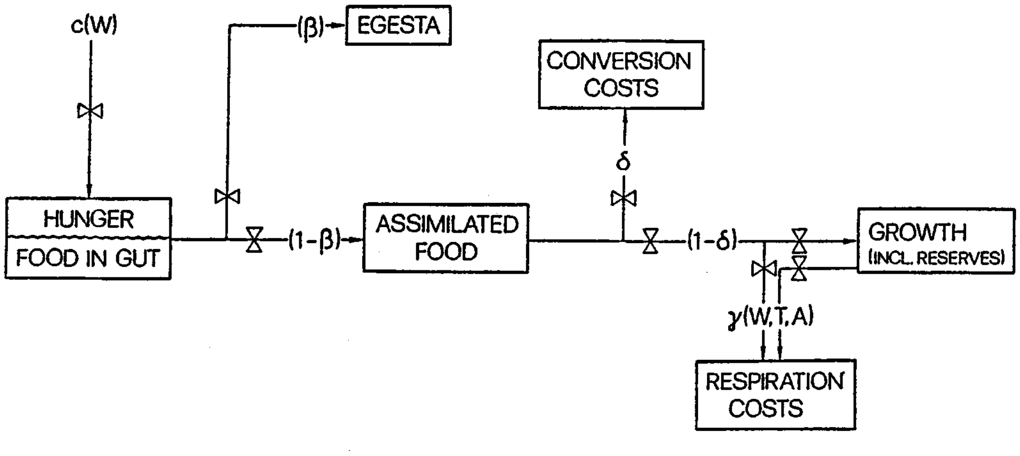

Fig. 1 The metabolic pool model adapted from **Gutierrez** and coworkers (1981, 1984a) to simulate growth and development of immature coccinellid life stages (c = food consumption rate ; β and δ = egestion and conversion ratios ; W = weight ; T = temperature ; A = activity ; γ = respiration rate).

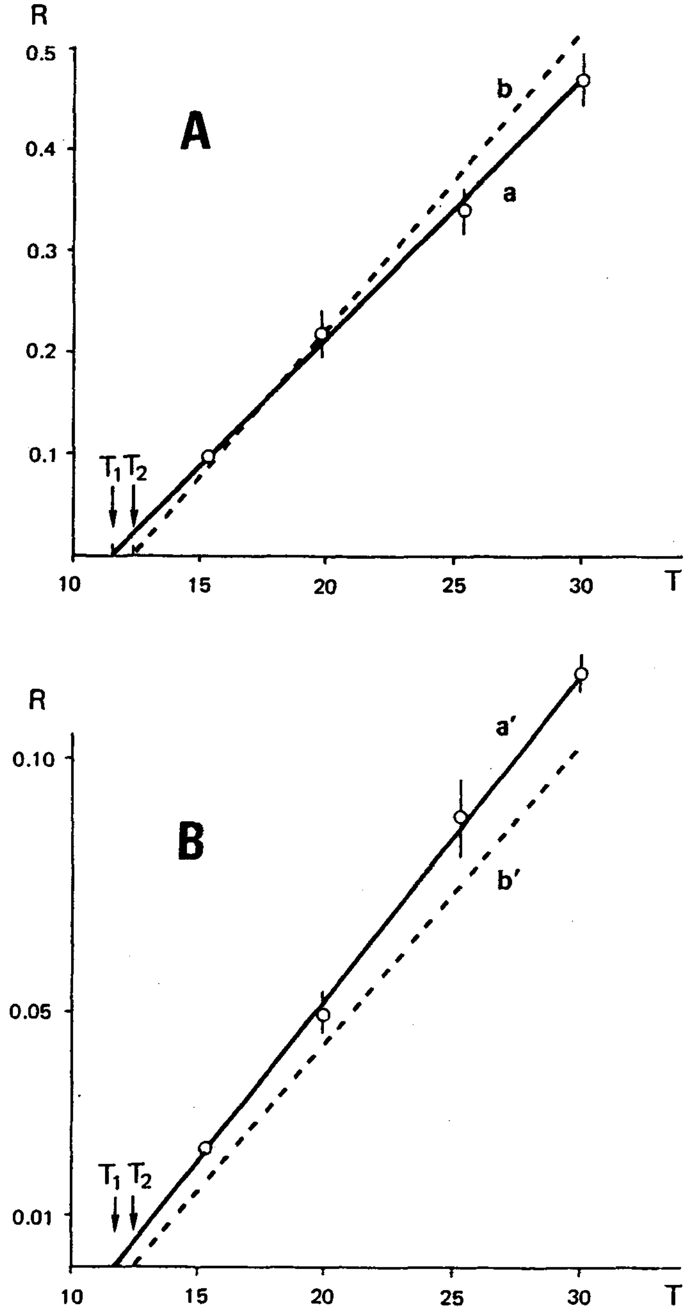

Fig. 2. Developmental rates ($R = 1/D$, D = duration in days) for eggs (A) and subsequent preimaginal stages (B) of *Propylaea 14-punctata* [a, a'] and *Coccinella 7-punctata* [b, b' ; based on the data of **Hodek** (1957)] as a linear function of temperature (T) (T_1, T_2 = lower developmental thresholds). The regression lines are $R = -0.288 + 0.025 \bullet T$ for a, $R = -0.073 + 0.0063 \bullet T$ for a', $R = -0{,}357 + 0.029 \bullet T$ for b, and $R = -0.072 + 0.0058 \bullet T$ for b'.

PHYSIOLOGICAL TIME AND PREIMAGINAL DEVELOPMENT

Hibernating adults of *Propylaea 14-punctata* L. were collected in Northeastern Switzerland at the beginning of May and fed ad libitum with *Acyrthosiphon pisum* Harris. The eggs obtained were exposed to 4 constant temperature regimes (15.3°, 19.8°, 25.3° and 30.0°C) and long day conditions (16/8 h). For each temperature 30 eggs were considered. At low temperatures (15.3° and 19.8°C), the preimaginal development was checked twice a day, while at high temperatures (25.3° and 30°C) it was observed 4 to 5 times per day. Larvae of the predator were also fed ad libitum with aphids at various stages of development. Developmental rates per day of preimaginal stages were plotted against temperature. Because the assumption of the homogeneity of variance failed (table 1 ; p = 0.01 ; **Engelmann**, 1981), the data from each experiment were weighted with the inverse of the variance, before fitting a linear regression model using the BMDP1R algorithm (**Anonym**, 1981). On the other hand, an unweighted linear regression was used to describe **Hodek**'s (1958) data relating developmental rates of *Coccinella 7-punctata* L. to temperature (fig. 2).

TABLE 1

Developmental rates (R) per day with standard deviations SD(R) for 30 eggs (E) and 30 subsequent preimaginal life stages (PI) of Propylaea 14-punctata *when offered a surplus of* Acyrthosiphon pisum *at various constant temperatures (T)*

T		R	SD(R)
15.3	E	0.0965	0.0051
	PI	0.0232	0.0011
19.8	E	0.2157	0.0150
	PI	0.0497	0.0026
25.3	E	0.3415	0.0218
	PI	0.0884	0.0081
30.0	E	0.4681	0.0276
	PI	0.1167	0.0044

Detailed life table information is available on *Coccinella 7-punctata* L. and life phases can easily be separated (fig. 5). No attempt was made to separate the prepupal phase from the pupal stage of *Propylaea 14-punctata* L. and the 2 were combined here in 1 stage called pupae.

PREY CONSUMTION, EGESTION, AND FOOD ALLOCATION

For egg production 40 adults of *Propylaea 14-punctata* L. were kept in small Petri dishes of 5.3 cm Ø (♀ per dish). Thirty larvae were reared individually in small aluminium boxes of 2.5 cm Ø and used for studies detailed below. They were maintained at standard conditions of 20°C, 70 to 90 % rh, long day (16/8 h). Each individual received water and 35 mg food (starving aphids) at least 3 times per day. The aphids which were not consumed were dried and weighed. From the time they were weighed until they were consumed the aphids lost weight. A correction factor was introduced for the calculation of the dry weight of the consumed aphids. The larvae of *Propylaea 14-punctata* L. were weighed immediately after hatching and after each moult ; at the same time the aluminium boxes were replaced and the egesta dry weight determined. The adults were weighed periodically, the Petri dishes replaced daily and the egesta collected, dried and weighed. It was calculated that 20 % of the larval egesta and 10 % of the adult egesta could not be recuperated from the rearing units, and figures were modified accordingly. The dry weight of the predator life stage, aphid prey and egesta were determined by first drying them at 40°C for 24 h and cooling them for 2 h at room temperature before weighing. The amount of food consumed by *Propylaea 14-punctata* L. is expressed as mg dry matter per mg predator dry weight and daydegree. The weight loss of *P. 14-punctata* eggs during the incubation period and hatching was used to approximate basic respiration costs (γ) at 20°C for inactive life stages of both species *P. 14-punctata* and *C. 7-punctata*. Thus, for non searching coccinellids γ is expressed in mg per mg predator dry weight at 20°C.

C. 7-punctata egestion was estimated by **Singhal** (1976), while food consumption was calculated with simulation experiments using **Blackmann**'s (1967b) results.

These observations enabled us to calculate the production (Δ W) as a function of assimilation. The nutritionists approach (**Bickel**, 1977) can be used to approximate conversion ratios (fig. 3) for both species.

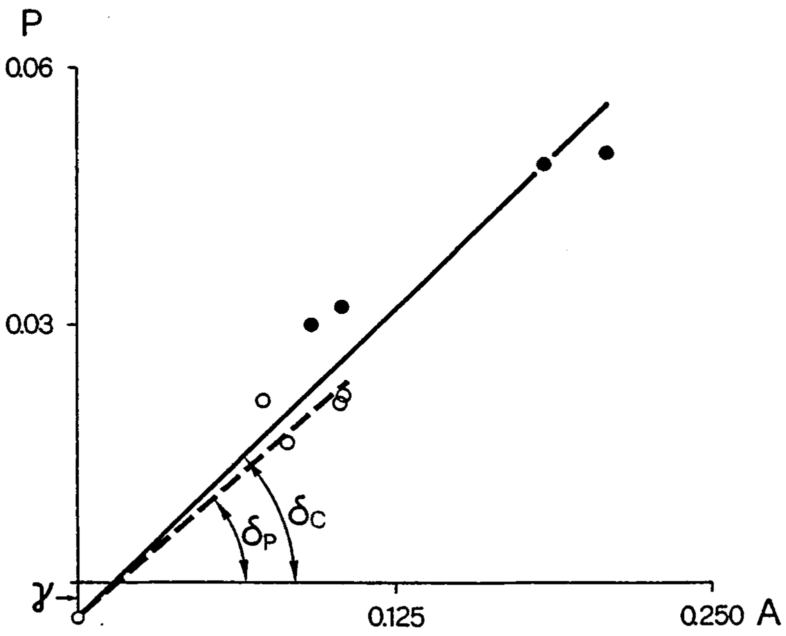

Fig. 3. The conversion of assimilated food (A) into production (P, i.e. growth) for larvae of *Propylaea 14-punctata* (δ_p = ratio) and *Coccinella 7-punctata* (δ_c = ratio) (δ_p = 0.26 ; δ_c = 0.29). Parameters for the latter species are estimated from the work of **Blackmann** (1976) and **Singhal** (1976). The regression lines are forced through a common intercept that represents basic respiration costs per mg dry weight of inactive *P. 14-punctata* kept under standard conditions (20°C, 70-90 % rh, 16/8 h photoperiod) (γ = 0.0042).

MODEL TESTING

The model is tested by visual examination of the calculated and observed pattern of growth and food consumption (fig. 4, 5).

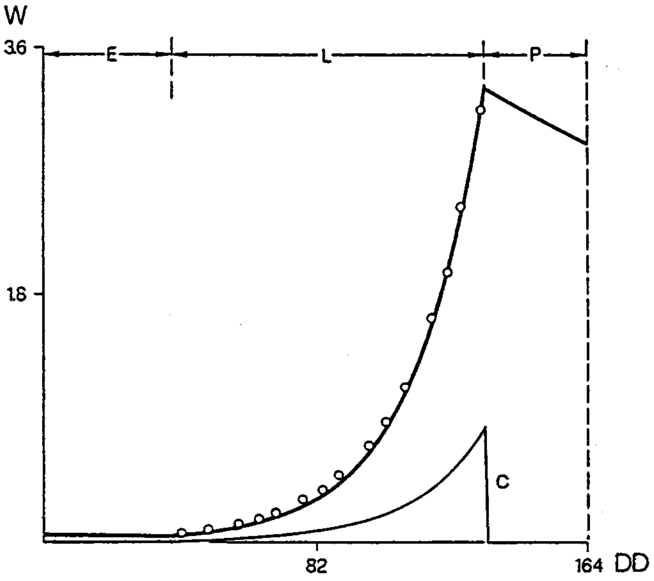

Fig. 4. Weight (W) and consumption rates (c) per daydegree (in mg dry matter) of immature life stages of *Propylaea 14-punctata* as a function of physiological time in daydegrees above a lower developmental threshold of 11.6°C (DD) (E = eggs ; L = larvae ; P = pupae including the prepupal stage ; o = observed ; – = simulated).

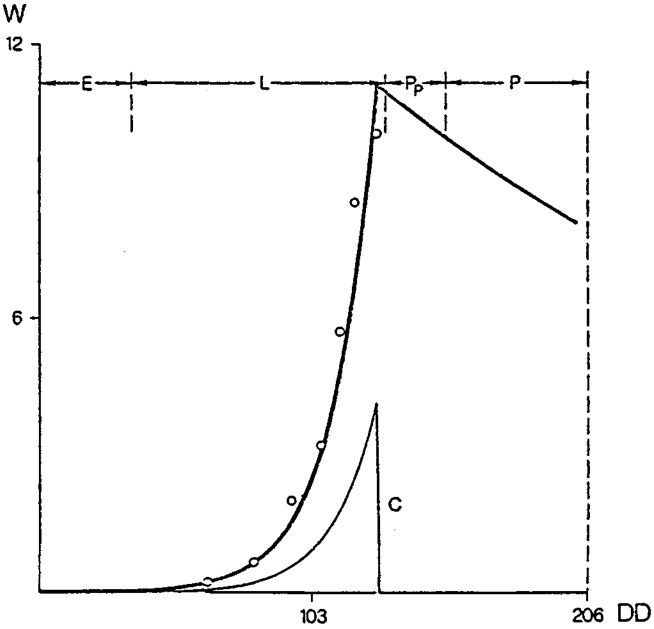

Fig. 5. Weight (W) and consumption rates (c) per daydegree (in mg dry matter) of immature life stages of *Coccinella 7-punctata* as a function of physiological time in daydegrees above a lower developmental threshold of 12.4°C (DD) (E = eggs ; L = larvae ; P_p = prepupae ; P = pupae ; o = observed ; – = simulated).

RESULTS AND DISCUSSION

PHYSIOLOGICAL TIME AND PREIMAGINAL DEVELOPMENT

The developmental rates (1 / D, D = duration in days ; table 1) of eggs (fig. 2, A) and subsequent preimaginal stages (fig. 2, B) appear to be linearly related to temperature in the range 15 to 30°C. Hence, the physiological time can be expressed in daydegrees above developmental thresholds, which are the same for all preimaginal life stages of a given species. The average thresholds of *P. 14-punctata* and *C. 7-punctata* [based on **Hodek**'s (1958) data] are 11.6°C and 12.4°C respectively, and in all further analyses physiological time is expressed in daydegrees above these thresholds. **Obrycki & Tauber** (1981) also observed linear developmental rates for *C. 7-punctata* in a comparable temperature range ; lower thresholds, however, varied between 6.8°C for eggs and 13°C for 1st instar larvae, while the threshold for the total preimaginal development was 12.1°C, which is very close to that observed in our experiments.

The egg stage and the following preimaginal development of *P. 14-punctata* takes 39.1 resp. and 25.1 daydegrees, those of *C. 7-punctata* 34.4 resp. and 171.6 daydegrees.

PREY CONSUMPTION, EGESTION, AND FOOD ALLOCATION

The average quantity of food consumed (c) per daydegree and per mg predator larvea dry weight was 0.26 mg for *P. 14-punctata* and 0.4 mg for *C. 7-punctata*, the latter estimated from **Blackmann**'s (1967b) work. These values are much higher than those calculated for the coccinellid *Hippodamia convergens* (G.-M.) preying on *A. pisum* (**Gutierrez** *et al.*, 1981 ; **Gutierrez & Baumgaertner**, 1984a, b). In *P. 14-punctata* the food consumption per mg predator dry weight tended to decrease with increasing body weight, and a similar relationship was found for much larger mammals (**Bickel**, 1977). The consumption rates recorded in this work correspond to the demand of the predator in the model of **Gutierrez** *et al.* (1981), and a functional response model can be used to model food acquisition under more general conditions.

Average egestion ratios (β) for *P. 14-punctata* and for *C. 7-punctata* are 0.32 and 0.36 respectively ; **Singhal**'s (1976) estimate for *C. 7-punctata* is close to those of the experiments with *P. 14-punctata*. These values are higher than those given by **Brafield & Llewellyn** (1982) who recorded an assimilation efficiency of 80 % for *C. 7-punctata*.

Both the parameters δ and γ (eqn. 1) are difficult to compare with the existing literature. This is due to the specific underlying model (fig. 1) and the procedures for parameter estimation. The respiration costs per daydegree and per mg predator dry weight were estimated for *P. 14-punctata* (γ = 0.00419) and used for both coccinellids. This is a crude estimate because the egg shell was not considered. **Randolph** *et al.* (1975) working with pea aphids were able to separate the losses of exuviae and respiration. The conversion ratios δ are calculated in figure 3 and values of 0.26 and 0.29 were found for larvae of *P. 14-punctata* and *C. 7-punctata*.

MODEL TESTING

Figures 4 and 5 show that the growth of both coccinellid larvae and the weight loss during the pupal stage are accurately represented by the model. Note that the curve represents the average weight of the life stages, disregarding possible differences between the 2 sexes. The values of the proposed model stems more from considering elements of nutritional physiology than from the exact estimation of physiological parameters and validation procedures. The latter are inadequate because part of the validation basis is also used for parameter estimation (see above). The method of relating production to assimilation for estimating conversion ratios enables us to consider nutritional theory when allocating assimilates in the coccinellid body. This procedure improves thereby the explicative qualities of the model without complicating its structure. This is particularly important when it is incorporated into a multitrophic system model as proposed by **Gutierrez** *et al.* (1984).

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ZUSAMMENFASSUNG

Simulation von Wachstum und Entwicklung juveniler Stadien von *Propylaea 14-punctata* L. und *Coccinella 7-punctata* L.[*Col. : Coccinellidae*] mit dem "metabolic pool" – Modell.

Aus der Beziehung Produktion (Wachstum) zu Assimilation (Beuteverzehr - Kotproduktion) wird das Umwandlungsverhältnis berechnet, mit dem Blattlausgewebe in Räuberwachstum umgesetzt wird. Als Beute für die Larven von *Propylaea 14-punctata* L. und *Coccinella 7-punctata* L. verwendete man die Erbsenblattlaus *Acyrthosiphon pisum* Harris. Die physiologische Zeit ist in Tagesgraden oberhalb eines unteren Entwicklungsnullpunktes angegeben. Für die beiden Coccinellidenarten wurden auf physiologischen Grundlagen Simulationsmodelle erarbeitet. Sie beschreiben das Wachstums und die Entwicklung eines Räubers und beruhen auf dem Konzept des von **Gutierrez** *et al.* (1981) vorgeschlagenen "metabolic-pool"-Modell. Die visuelle Beurteilung von beobachteten und berechneten Werten zeigt, dass das Modell das Wachstumsmuster der erwähnten Räuber auf befriedigende Weise beschreibt.

SCHLÜSSELWÖRTER : *Propylea 14-punctata, Coccinella 7-punctata,* Simulationsmodell, Wachstum, Entwicklung, "metabolic pool".

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