HIERARCHICAL MODELLING OF PREDATOR-PREY RELATIONSHIPS IN AN ACARINE SYSTEM

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Introduction

The aim of this study is the construction of predator-prey models for field use. These models describe, as such, a sub process in the population models for the fruit tree red spider mite (Panonychus ulmi) - predacious mite system (Rabbinge and v.d. Vries, 1974).

In these models only population densities of the fruit tree red spider mite below the economic damage level are considered. This regulation below this level seems to be possible with predacious mites (Rabbinge, 1975). Regulation means then that the predacious mites cause a sufficiently increasing mortality rate when the prey density (P-ulmi) increases. In the fruit tree red spider mite - predacious mite system, (Panonychus ulmi - Amblyseius potentillae) three predator "species" (protonymphe, deutonymphe and adult females) and four prey "species" (larvae, protonymphe, deutonymphe and adult females) can be distinguished, the preference for the different stages depending on the state of the predator. The complexity of these interrelationships requires a detailed analysis of the predation process and in this introduction is shown how such a detailed analysis may lay the basis for a simple formulation of the predator-prey relationships in the higher ordered population models.

Modelling of predator-prey relations

Detailed analysis of predator-prey systems are given by several authors. Holling (1966) gave a general description of the predation process and developed a mathematical model which provides an explanation of the three fundamental types of functional response curves he distinguished. In these models searching periods are calculated as a function of the state variables at the beginning of searching, such as the hunger level, the gut content, of the predator. However these variables change during searching and so do the searching periods. Therefore computations of the values of the state variables at the beginning of the periods are not sufficient so that the general applicability of Holling's analytical models is questionable. Fransz in his simulation models, in which more flexible numerical integration methods are used by application of Continuous System Modeling Program (CSMP), a simulation language developed by IBM (1968), took this in consideration and paid also attention to the stochastic character of the predation process with a single predator and the changing of rates during the process.

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The predation process

The predator-prey system analysed in detail by H.G. Fransz (1974) consists of disks of 5 cm^2 of the leaves of the lima bean, placed upside down on wet cotton wool in Petri-dishes, with a number of fresh eggs of Tetranychus urticae and/or adult males and one to three ten days old Typhlodromus occidentalis female. In figure 1 a conceptual model of this predator-prey system is given. The system consists of one Typhlodromus occidentalis female on a leaf disk with constant numbers of Tetranychus urticae males and/or eggs. The elements of the predator-prey system are represented by blocks and the relationships by arrows. The number of captures per time unit (predation rate) depends on the number of encounters per time unit (encountering rate) and the success ratio (number of successful encounters divided by the number of encounters).

The success ratio is influenced by the hunger level of the predator, the gut content, and the frequency of encounters which may induce response waning, termed inhibition by prey by Holling (1966). The gut content of the predator is affected by the encountering rate, the feeding time and digestion. The only state variables in this system are the density of the prey i.e. the Actual Number of Eggs (ACNE), the Actual Number of Males (ACNM), the GUTCONtent of the predator adult female, the total distance covered by the prey males on the leaf disk (DIST) which determines the webbing density, and the indicator of the engagement of the predator (H) which is one when it is handling prey and zero otherwise. The other factors are rate variables or auxiliary variables.

Simulation

The conceptual model is used to build mathematical models of the system with the purpose to understand the predation process. The state variables considered e.g. the gut content and the webbing density vary with time because they depend on processes like ingestion, digestion and locomotion. As a consequence other system elements change because they are determined by the state variables.

The number of prey killed per time unit is also not constant, and the models are used to simulate the dynamics of the system at different prey densities and to compute the expectation values of the numbers of prey killed per predator and other output variables as a function of time.

In fig. 2 a time film of the predation with a single predator is given. A predator may start searching (H=0, S=1) at time zero. At the time t_1, it may catch a prey (catch=1.) to start a period of handling prey (H=1, S=0). The capture of a prey may take some time (CATIM). To account for this a state variable RCTIM will be introduced. RCTIM is set equal to CATIM at the beginning of a handling period, and decreases with time until it is zero at the end of CATIM. At the end of CATIM at t_2 the predator starts feeding. This increases the gut content (GUTCON), but decreases the content of the prey egg (EGG). At t_3 the prey is empty and up till to the next feeding period, GUTCON decreases by digestion. At t_4 the predator abandons the prey (ABAND=1.) to start a new searching period. At t_5 a second prey is captured, which may be abandoned before it is emptied.

Ingestion and digestion

The rate of decrease of the gut content is assumed to be exponential that is equal the gut content multiplied with the relative digestion rate DIGEST, a parameter that only depends on the temperature, which is here kept constant.

The ingestion rate (INGRT) of the predator depends on

1. whether the predator is handling or searching prey (whether H equals 1 or 0)
2. whether it actually feeds on the prey handled (RCTIM equals 0)
3. on the content of the prey. (EGG or Male greater than 0)
4. on the gut content of the predator.

It is assumed that the ingestion rate dA/dt is proportional to the difference between the actual gut content (A) and the maximum gut content (M): $dA/dt = c * (M-A)$, where c is a positive constant. Calculations with experimentally determined values of A and t showed that M is 1.08 egg equivalents and c is 1.32 min^{-1}.

Stochasticy of the predation process

The integer H is initially zero and becomes 1 when the predator catches a prey (CATC=1.). H becomes zero again when the prey is abandoned (ABAND=1.). CATCH and ABAND are random variables which may become 1 or zero during a time interval. The process of catching has been observed to be a Poisson process. Irrespective of handling time, the number of prey caught in Δt has a Poisson probability distribution, with average values $s E \Delta t$, s being the success ratio, E the average number of encounters per time unit. This number depends on the actual number of eggs (ACNE) on the leaf disk, the coincidence in space (COINA), the locomotion velocity of the predator (VELPRE) and the activity of the predator (ACTPRE):

$E = ACNE * VELPRE * COINAE * ACTPRE$.

Also the abandonment of the prey is a Poisson process; during each time step there exists a small probability that the predator leaves its prey. This probability seems to be determined by hunger in the first place, since hungry predators continue feeding on empty preys, while satiated predators abandon their prey even when it is not empty (fig. 3).

Deterministic simulation of the predation process is reached when the variables H, S, CATCH and ABAND, which represent conditions and events in a stochastic model are considered as proportions on a continuous scale of individuals in a population, which in fact are subjected to these events or conditions. Also the probability of abandonment PRA and the probability of catching PRC are considered to be proportions and all other variables represent population means. The stochastic models give good results, but requires an excessive amount of computing time. The deterministic model requires much less computing time, but its results are wrong, because of the many curvilinear relationships that are involved (fig. 4). A new method, compound simulation, has the advantages and disadvantages of both buth the latter on a permissable level. It is a deterministic model which provides the expectation values of the stochastic model, but with much less computing time. Basically, this is achieved by applying every time step the deterministic model to homogeneous classes of individuals which are then de-homogenized, but reclassed again and again. Some results of compound simulation are given in fig. 5 in comparison with the results of independent verification experiments. In this way an explanation for the functional response of the predator to prey density is given from the underlying physiological and ethological processes.

Prey utilizing and numerical response

The utilization of the prey is computed with the compound model. It depends to a large extent on the gut content and because of the observed relation between the gut content of the predator and its fecundity (Fransz, 1974) the numerical response to prey density may also be derived from the computed gut content of the predator.

Predation process in population models of the fruit tree red spider mite system

The models on the predation process explain this process and provide the basis for its incorporation in the population models. In the fruit tree red spider mite - predacious mite system three predator "species" and four prey "species" are distinguished (larvae, protonymphe, deutonymphe and adult female of the prey and protonymphe, deutonymphe and adult female of the predator). In the population models the expectation values of the numbers of prey and predator are calculated. Calculations with the complex compound model made clear that the system reaches an equilibrium within a few hours, which means that the gut content of the predator oscillates with a small amplitude on a level, depending on predator and prey-density and the temperature of the system.

Therefore it is not necessary to use this complex model in population models at a higher hierarchical level. It suffices to work with the expectation values of prey risk and prey value as a function of the state variable that characterizes the hunger level of the predator. Prey risk in time^{-1} gives the risk of each individual prey to be caught, prey value for instance in units of gut content per killed prey expresses the utilizing and the preference of a prey. The quantification of the hunger level of the predator is here easy, because well fed predators show a dark reddish colour, while hungry predators are whitish and transparant. A colour scale was developed which relates the behaviour of the predator (success ratio) and the quantity of leaf and animal pigments in the predator, that cause the colour. The dependence on temperature of the relative digestion rate or Relative Decrease of the Condition Variable (RDCV) is quantified in thermostat experiments. The ingestion rate or the rate of increase of the condition variable (INCAF) depends on the prey risk and the prey value, both being gut content dependent and on the density of the prey and the predator. In case of one predator "species", A. potentillae adult female, and one prey "species", P. ulmi adult female, this is written in Continuous System Modelling Program:

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DECAF = RDCV * CTAF
INCAF = RISAF * PAF * TTAF * PV
CTAF  = INTGRL (5., INCAF - DECAF)
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DECAF = rate of decrease of the condition variable
CTAF = Condition Typhl. Adult Female
RISAF = RISK Panonychus ulmi Adult Female
PAF = number of Panonychus ulmi Adult Female
TTAF = Total number of Typhlodromus Adult Female
PV = Prey Value

In the equilibrium situation the prey risk is calculated as $\frac{\text{predation rate}}{\text{prey density}}$, when TTAF = 1. per unit of surface.
Since in the equilibrium state

DECAF = INCAF,

the prey value equals

$$PV = \frac{RDCV * CTAF}{RISAF * PAF * 1.}$$

The in this way experimentally found relations, prey risk in dependence of temperature and condition variable, prey value in dependence of condition variable, and relative decrease of the condition variable in dependence of temperature are input relations for the population model. This way of programming the predation process makes preference experiments superfluous as is demonstrated by the agreement of simulated and experimental results of a system with P. ulmi larvae and P. ulmi females in figure 6. The dependence of the numerical response on the condition variable is found by other experiments. In this way the complex predator-prey relationships are incorporated in a very simple way in the population models, without loosing any of the explanatory value of the models, because they are based on a detailed analysis of the predation process. The results of the population models and their possible application in the field are discussed by Rabbinge (in prep.) in a description of the models and their results.

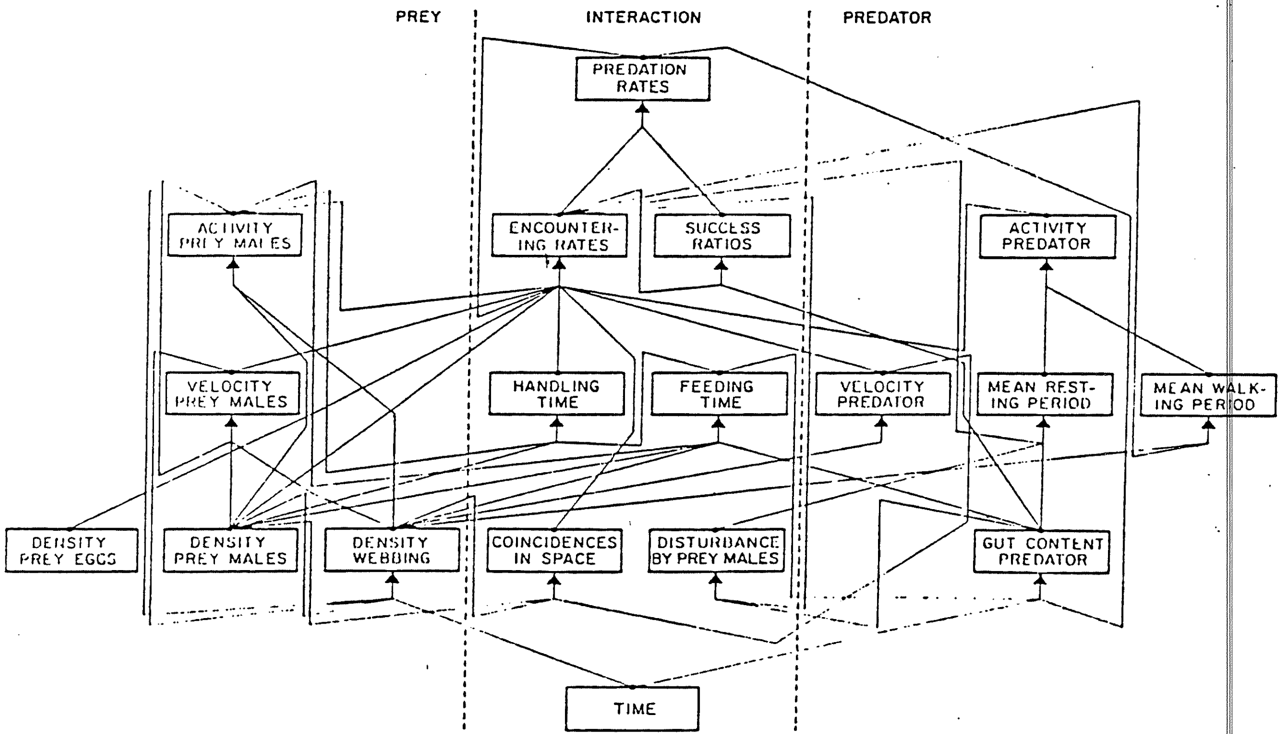


Fig. 10 | Conceptual model of a predator-prey system. One *Typhlodromus occidentalis* female on a leaf with constant numbers of *Tetranychus urticae* males and eggs.

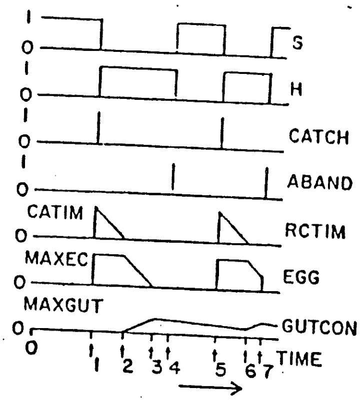


Fig. 12 | A time film of the preda process with a single predator.

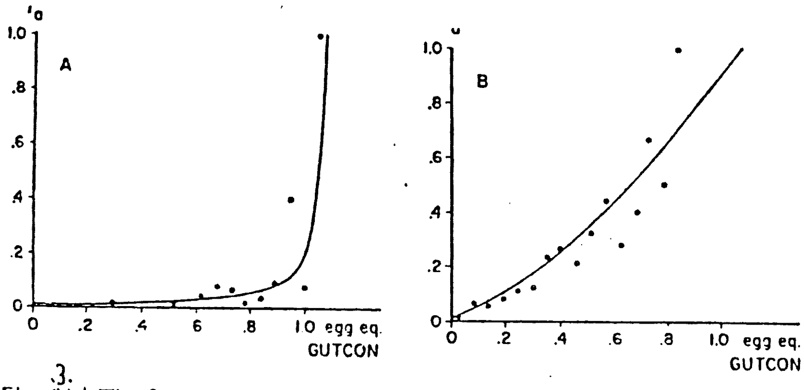
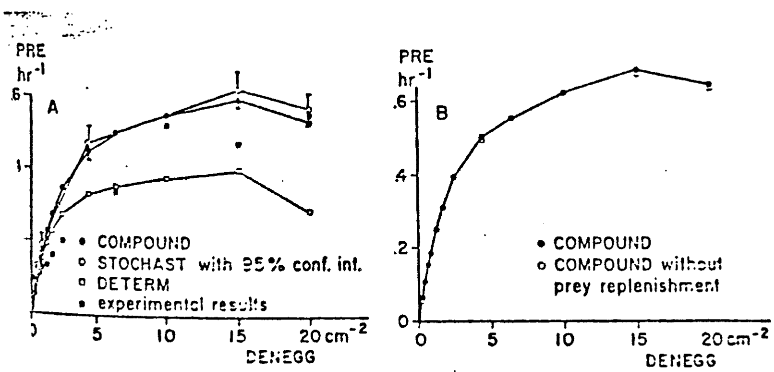


Fig. 3. | The frequency of abandonments as related to the gut content when the predator handles eggs (A) or males (B).



4 | The functional response to the egg density for the last six hours (A) the first six hours (B) of a 24-h period.

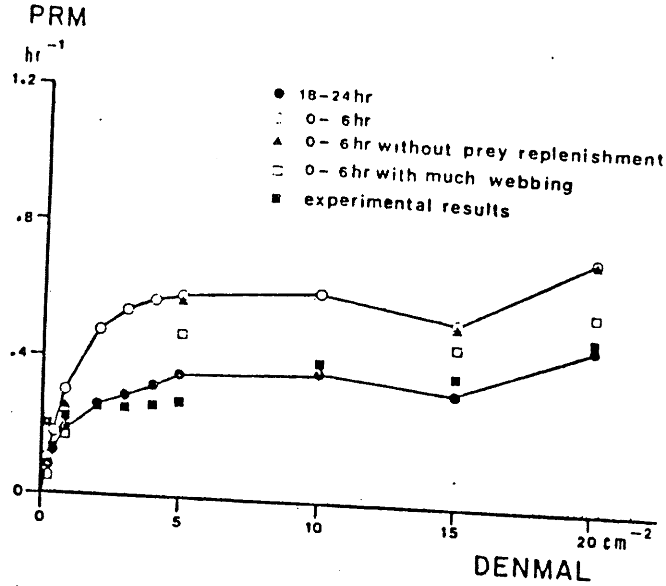
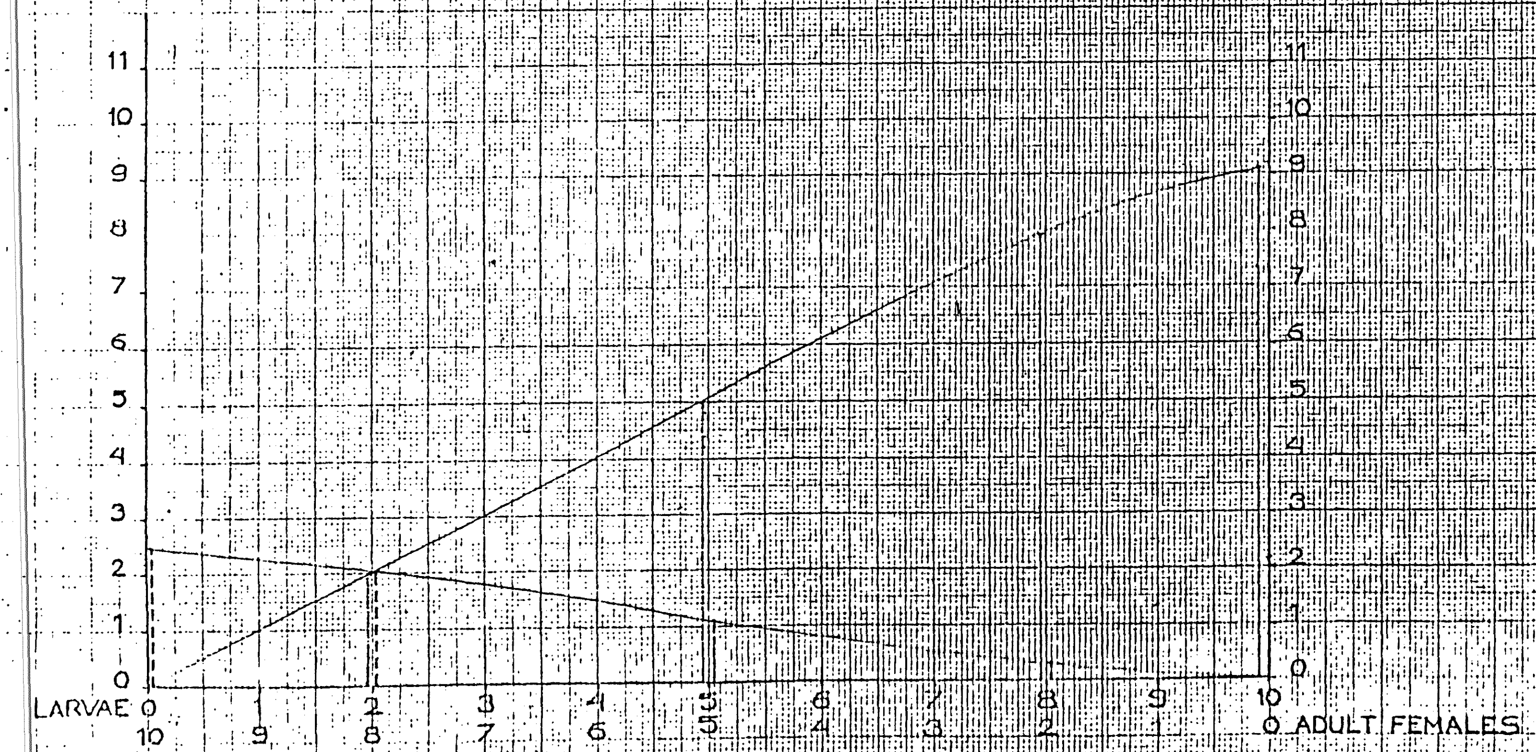


Fig. 5 | The functional response to male density as computed b
program COMPOUND, and obtained by independent experiments.

PAF	PPL	Pred. P.P.L	Pred. PAF	CTAF
10 –	0	0.	2.39	2.44
8 –	2	2.	2.17	4.6
5 –	5	5.	1.09	5.0
2 –	8	7.9	.3	5.5
0 –	10	9.1	0	5.67



PREDATION OF LARVAE AND ADULT FEMALES

FIGURE 6